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Synopsis of the Supraspecific Classification of Living Oysters (Bivalvia: Gryphaeidae and Ostreidae)

by

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Abstract. Recent members of the superfamily Ostreacea are subdivided into two families, four subfamilies, ten tribes (all new) and 24 genera and subgenera (12 new). Based on the examination of the gross anatomy of the flesh of all but four of the 36 known species of living oysters, and the shells of each, the supraspecific units are defined sufficiently to differentiate coordinate taxa. Illustrations are provided of the shells of type species of the new genera and subgenera, as well as of significant anatomical features. Two junior homonyms are renamed at the species level.

IN STUDYING the large collection of oysters of the U.S. National Museum of Natural History on several visits during the last few years, and other material collected by myself or provided by many friends, I have found it necessary to extend the classification of the living species beyond that proposed by STENZEL (1971), in order to indicate their diversity and relationships more precisely. The purpose of the present synoptic account is to remedy the deficiency by introducing several new taxa at the level of subgenus, genus, and tribe. The type species at the generic level are described and illustrated in sufficient detail to differentiate them from coordinate taxa and to give them nomenclatorial validity. Other species within genera having multiple species, although listed, are not treated in such detail. Complete bibliographic references to previously established genera and their types, as well as illustrations of the latter, are to be found in STENZEL (1971); references to the proposed nominal species of living oysters are provided by LAMY (1929–1930) and HARRY (1981). Because the limits of morphological variation, habitat, and zoogeography of most species are poorly known, a more extensive account, discussing those factors and the complicated synonymies, must await further study.

The shells of all species, and the flesh of most, have been available for study. Several new characters have thereby been discovered, some of which were briefly noted in two short abstracts (HARRY, 1981a, 1983). TORIGOE (1981) independently found some of these new characters. Considering not only the structure of the flesh and shell but also the environments, geographic range on a worldwide basis, and behavior (habits) of oysters produced more character series (see HARRY, 1968, 1971) than are usually used in systematic works on bivalves. Although no new species are proposed, apart from renaming two junior homonyms, it is necessary to introduce new taxa at several levels in order to express the degrees of relationship, or classification, adequately. Such a procedure is inevitable, as pointed out by SCHENK & MCMASTERS (1948:3) and CROWSON (1970).

STENZEL's (1971) classification has been reviewed and somewhat modified by HARRY (1981), TORIGOE (1981), and HARRY & DOCKERY (1983). Torigoe elevated one subfamily of the three that Stenzel recognized in the Gryphaeidae to family rank, Pycnodonteidae. This seems of little use, and merely confuses the issue of relating the two extinct subfamilies, Gryphaeinae and Exogyrinae, to the Pycnodonteinae. On the other hand, Torigoe recognized the need of separating *Crassostrea* and related genera from the Ostreinae as the subfamily Crassostreinae, a step foreshadowed by Stenzel in his arrangement of genera, but not definitely taken by him. Torigoe followed Stenzel in placing the Lophinae after the Ostreinae (and Crassostreinae); but the Lophinae share with the Pycnodonteinae several characters which are absent or much modified in the Ostreinae. Conversely, new characters appear in the Lophinae which are shared with the Ostreinae and Crassostreinae, but are absent in the Pycnodonteinae, and additional characters appear in the Ostreinae which are shared only with the Crassostreinae. Details supporting this arrangement are summarized after the definitions of the appropriate subfamilies.

In some of the earlier literature on the anatomy of oysters there was much confusion about their proper orientation (see below, "promyal passage"). In this paper the hinge is considered to be dorsal, and when one has the outer surface of the right, or unattached, valve facing them, with the hinge uppermost, the anterior margin is to the right, the posterior one on the left, and the ventral margin is opposite the hinge. This orientation was used by Galtsoff (1964) and Stenzel (1971), in whose works general anatomical accounts of oysters are presented. The height of a specimen is measured along a line perpendicular to the axis of the ligament, and length along a line perpendicular to the height and parallel to the ligamental axis. Small oysters are those whose maximum dimension (usually height) is about 30 mm or less; medium sized ones extend to about 50–70 mm; and larger ones are greater than that size. Normal oceanic salinity is 35 parts per thousand (ppt), varying about 2 ppt; in warm climates some restricted bodies of water may have salinities that are several ppt higher than normal (Red Sea, Persian Gulf, *etc.*). In brackish water the salinity is usually much lower, and more variable, than where normal salinity prevails. USNM refers to the collection of Recent mollusks of the United States National Museum of Natural History.

The intraspecific variation of oyster shells, which is probably greater than in any other group of living bivalves, precludes the preparation of a simple and satisfactory taxonomic key. The systematic format presented below should allow the identification of any living species to the generic level, or lead to the conclusion that it belongs to an undescribed genus. However, this requires that one know considerably more about the species to be identified than the limited characters inherent in a single dry shell, such as that which is usually thrust on some presumed authority for an immediate identification, or subjected to a taxonomic key. Moreover, the format here presented goes beyond the taxonomic key, because the first entry (superfamily definition) allows the exclusion of several oyster mimics, such as species of *Anomia, Plicatula, Spondylus, Hinnites, Chama* and related genera, as well as other monomyarian bivalves such as the sponge oysters (Vulsellidae), pearl oysters (Pteriidae), hammer oysters (Malleidae), and indeed of all other bivalves of the order Pterioida. Three tables are appended to summarize the more prominent variable characters of the true, or common, oysters of the two families Gryphaeidae and Ostreidae.

I am much obliged to the personnel of the U.S. National Museum of Natural History, particularly Joseph Rosewater, Harald Rehder, Richard Houbrick, Thomas Waller, Frederick Bayer, and Druid Wilson, for their generous hospitality while I studied there. To B. J. Gallaway and Marion Fischel of the LGL Ecological Research Associates, Bryan, Texas, I am indebted for numerous specimens from offshore oil drilling platforms in Louisiana, which initiated my present study of the systematics of oysters. For her assistance in studying the oyster collection of the British Museum of Natural History I thank Solene Morris, and also Thomas E. Pulley and Constance E. Boone for their help in studying the growing mollusk collection and library of the Houston Museum of Natural Sciences.

Constance E. Boone also generously loaned oysters, which she personally collected, with most material preserved with flesh, from West Africa, Mauritius, Australia, the Philippine Islands, Fiji, Tahiti, the Tuamotu Islands, Gulf of Mexico, and western Mexico, as well as other lots of shells which she had obtained by exchange.

To John W. Tunnell, Jr., I am very obliged for making available a collection of 34 lots of oyster shells, of 14 species, which had evidently been assembled about 1950 by personnel of the Texas Game and Fish Commission at the Rockport Laboratory, where they had since been stored. This collection is now in the custody of the Biology Department of Corpus Christi State University. He also loaned much oyster material in alcohol, which he had collected in western Florida, and in the Persian Gulf.

Others who have provided significant material and information are: C. A. Beddinger, Tom and Beatrice Burch, Thomas Calnan, Hays Cumins, David T. Dockery III, Valerie Ernst, Mario Lasta, Paul and Paula Mikkelsen, Bryan Morton, Ellen J. Moore, Takeshi Ogawa, Juan Parodiz, Hugh Porter, Eric Powell, Dale Steinke, Jose Stuarto, and Margaret Teskey; to all of them I express my heartfelt thanks. [illegible]

Superfamily OSTREACEA Rafinesque, 1815

Bivalve mollusks (Order Pterioida, Suborder Ostreina) that are epifaunal, and in which the shell is usually attached by cementation of its left valve to a firm substrate, during at least early post-larval life (exception: ***Cryptostrea***). The shell shape is varied and irregular, conforming to the situation. The umbos may be small and inconspicuous, in which case they are nearly equal in size, but the left one varies from only slightly to many times larger than the right in some species. The shells are usually nearly equilateral, but inequivalve, and the left valve is generally more inflated. The umbos are usually opisthogyrous but they are often orthogyrous or prosogyrous, even within a species, among shells of adjacent specimens.

The periostracum is thin, smooth, nearly colorless, and quickly deciduous beyond the shell margin (possibly excepting ***Cryptostrea***). The prismatic shell layer is always present, either forming a continuous sheet or thin, projecting lamellae (sometimes thickened by the foliar layer). The lamellae may be closely spaced and imbricate, or reflexed to varying extent, and in some instances they form subcylindrical, tubular spines of varying length, called hyote spines. The inner, or foliar shell layer, is vitreous and translucent when thin and homogeneous (subnacreous in *Striostrea* and ***Pustulostrea***), becoming white and opaque when thicker. Besides the myostracal shell, underlying the adductor muscle attachment and progressively enclosed in the foliar layer as the shell grows, several other interruptions of the foliar layer may occur, depending on the species: in a process of chambering, the surface of a mantle lobe is pulled away from the foliar layer, then secretes a new layer, leaving a hollow space between the two; non-cellular, organic patches (conchiolin) of varied size, shape and thickness may be secreted, especially in more erodable shells (*e.g.,* **Striostreini**) and as an initial covering to shell injury; this layer is light green when thinnest, becoming light to dark brown when thicker. Pure white or colored, irregular, chalky deposits of varied size and thickness may also form.

The basic color of the shells is white or grayish, and shells of small species and the spat of larger ones may be golden brown from the organic material of the prismatic layer. The shells may be variously washed or radially striped with red or blue pigment, or a purplish combination thereof. Green or brown washes internally seem to result from covering the organic patches noted above. The color is highly variable within most species.

The functioning part of the ligament is an elongate, thin, semicylindrical mass extending before and behind the umbos (thus, it is amphidetic), along the hinge of the shell, with the convex surface facing the interior. Its internal surface is continuously increased along its length and at both ends. Above the inner surface the functional ligament is gradually superseded, losing its elasticity and becoming brittle; this part is external, and attached to a variable extent to a triangular ligamental scar on the medial face of each valve, below the umbos. From much of this scar the ligament is usually worn away. The ligamental scars are divided vertically into three equal triangular parts, the central resilifer and anterior and posterior bourrelets (except in the extinct subfamily Exogyrinae: see HARRY & DOCKERY, 1983).

There are no hinge teeth comparable to those of most other bivalves, but most species of oysters have some form of ridges or pustules along the margin of the shell. These are usually near the ligament when present, sometimes limited to a short strip there, but often extending downward on anterior and posterior shell margins for a variable distance, and even across the ventral margin. These marginal denticles, collectively called chomata by STENZEL (1971), are of systematic importance. They are all apparently derived from faint structural bands which are narrow, parallel to each other, and normal to the shell margin; these can be seen on the surface of the foliar shell layer in an occasional specimen of many species. They are here termed *protochomatal* bands. In *Alectryonella* they are generally present and much exaggerated.

Post-larval oysters are monomyarian, retaining only the morphologically posterior shell adductor muscle, which is placed posteroventrally; it is divided into "quick" (translucent, dorsal) and "catch" (opaque, ventral) parts. The shape of this muscle is indicated in the scar it leaves on the inner surface of the shell, and the shape varies significantly at the level of families and some lower taxa; but the two parts of the muscle seem never to be shown in the scars.

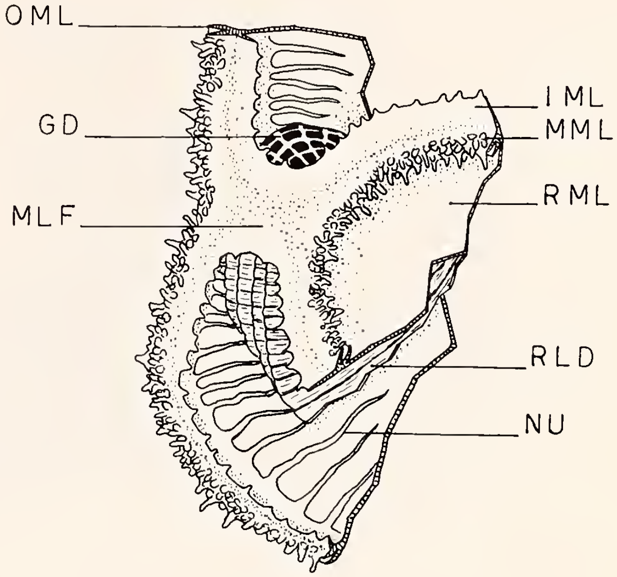

Figure 1

Fusion of mantle lobes at posteroventral curve of shell. From a specimen of *Crassostrea virginica* from Galveston, Texas; accessory heart not shown (hidden by diaphragm). GD, gill diaphragm; IML, inner mantle margin lamella; MLF, mantle lobe fusion; MML, middle mantle margin lamella; NU, neobranch unit; OML, outer mantle margin lamella; RLD, right lateral demibranch of gill; RML, right mantle lobe.

The foot is entirely lost early in post-larval life, when the larva settles and attaches. This condition of early foot loss is here termed *paedapody,* to emphasize its near uniqueness in this group (possibly also occurring in Dimyidae?) and the several distinctive morphological features resulting from it. Nearly all other bivalves that experience foot loss or atrophy (an occasional species in several distantly related families) do so late in post-larval life, a condition here termed *gerontapody.* The usual superficial musculature of the visceral mass, both the sphincter component which functions to extend the foot, and the rectilinear pedal retractors, is absent throughout post-larval life of oysters. Small, short gill protractor muscles are generally prominent in oysters, attaching to the shell below the umbos, where they may leave a scar; these were named Quenstedt's muscles by STENZEL (1971:N965), who mistakenly considered them to be remnants of pedal retractor muscles.

Besides the usual confluence of the mantle lobes below the hinge (the isthmian mantle, which secretes the ligament), they are only fused to each other elsewhere by short extensions of the inner mantle margin lamellae at the posteroventral curve of the shell margin (Figure 1); the potential excurrent opening thus occupies the whole of the

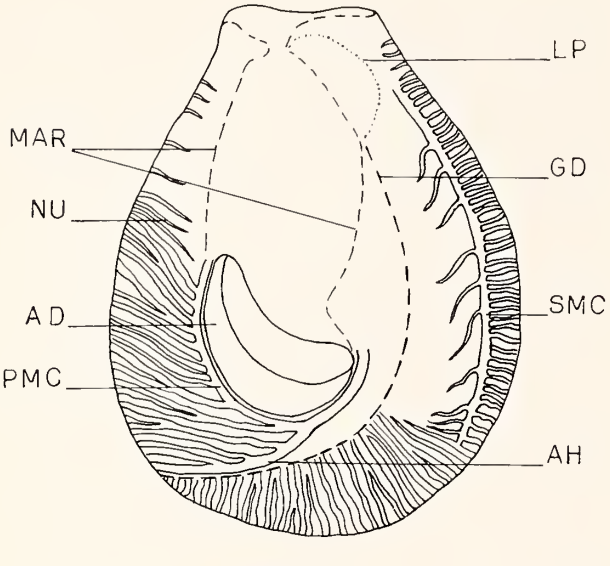

Figure 2

Diagram of the neobranch of left mantle lobe of *Ostrea puelchana* from Port Phillips Bay, Victoria, Australia (USNM 767650). AD, adductor muscle; AH, accessory heart; GD, gill diaphragm; LP, labial palp; MAR, limit of attachment of right mantle lobe to visceral mass; NU, neobranch unit; PMC, perimyal collecting vessel; SMC, submarginal collecting vessel.

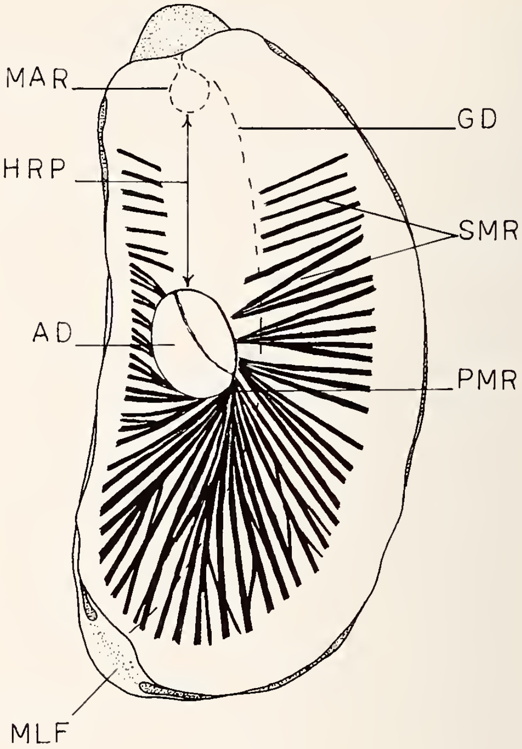

Figure 3

Distribution of pteriomorph mantle margin retractor muscles, diagrammed from a specimen of *Neopycnodonte cochlear* from Algiers, Algeria, loaned by H. B. Stenzel. Marginal papillae not shown. AD, adductor muscle; GD, gill diaphragm; HRP, height of right promyal passage; MAR, limit of attachment of right mantle lobe to visceral mass; MLF, mantle lobe fusion; PMR, primary mantle margin retractor muscle; SMR, secondary mantle margin retractor muscles.

posterior shell margin, the incurrent opening both the ventral and anterior parts of the margin.

The margin of each mantle lobe is divided into three lamellae. The inner mantle margin lamella is only moderately high, and in life it stands at right angles to the mantle lobe; along its free margin there are small, tapering papillae, usually separated by a space several times as long as their diameters; the middle lamella is held parallel to the mantle lobe's surface, forming between it and the outer lamella a narrow, shallow periostracal groove. The outer mantle margin lamella, as in all bivalves, is without papillae. There are no papillae along the free margin of the middle lamella, but its medial (exposed) surface is densely set with long and short, tapering papillae, irregularly arranged. Contrary to Torigoe (1981) and previous workers, I have not found the size and arrangement of these papillae to be of systematic value.

In both incurrent and excurrent mantle chambers, submarginally along the medial surface of both mantle lobes, there are tubular ridges, normal to the mantle margin. These begin shortly below the isthmian mantle junction, increasing in size and becoming more closely spaced toward the ventral margin. They taper inward, occasionally branching at one or both ends. They are protrusions of vascular recessions (or "blood vessels," although undefined by special cells lining their interiors) of the parenchymatous tissue between the two epithelial layers bounding the surface of the mantle lobes. These tubes are here termed *neobranch units,* and collectively termed the *neobranch,* structures universally present but hitherto unnoticed in oysters (Figure 2). In the incurrent mantle chamber there is usually a longitudinal protruding vessel in each mantle lobe, parallel to the mantle margin. These begin near the isthmian mantle, some distance inward from the margin, which they parallel to a rather abrupt termination at the anteroventral curvature of the shell margin. There, these *submarginal collecting vessels* disappear in the musculature of the mantle margin.

No such submarginal collecting vessels are present in the excurrent mantle chamber, but the neobranch units immediately behind and above the gill diaphragm, in each mantle lobe, are often enlarged. Such enlarged neobranch units extend inward along the anterior margin of the adductor muscle, where they fuse with other vessels (venous) from the ventral ends of the axial suspensory septa of the gills (explained below), and occasionally with a circummyal vessel along each margin of attachment of the adductor muscle (Figure 2), immediately before entering the

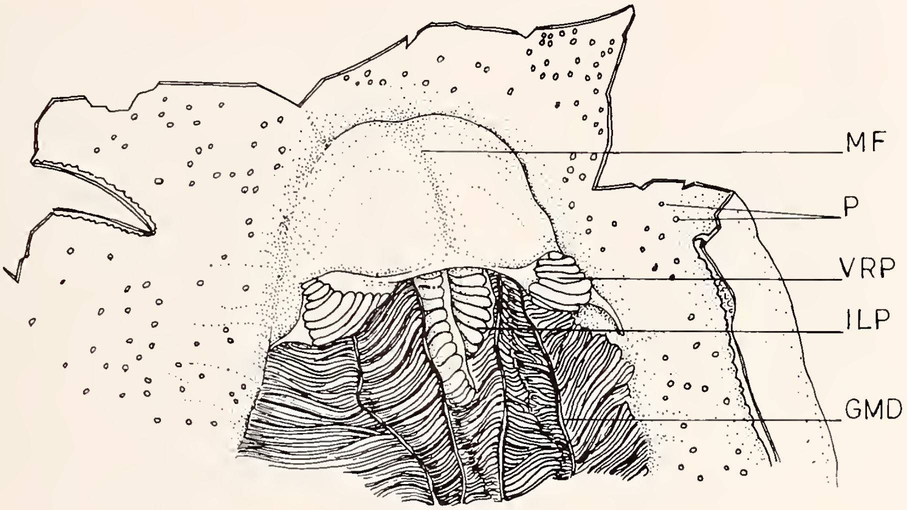

Figure 4

Labial palps of *Neopycnodonte cochlear*. Specimen from Algiers, Algeria, loaned by H. B. Stenzel. GMD, groove on free margin of demibranch; ILP, inner labial palp; MF, median fusion of outer labial palp; P, papillae on inner surface of mantle; VRP, reflected tip of outer labial palp.

auricles of the heart. When enlarged and passing forward to enter the heart, the two post-diaphragmal units of the neobranch are known as accessory hearts. They pulsate, carrying blood to the heart auricles. Whether the accessory hearts receive as tributaries the several adjacent neobranch units varies at the generic level (Figures 2, 5). The most recent extensive account of the accessory hearts, by GALTSOFF (1964, *q.v.* for references to earlier works) is incorrect in many details.

Besides muscle fibers in the mantle lobes adjacent and parallel to the mantle margin, which subtend the three mantle margin lamellae and constitute circular musculature, there are also mantle margin retractor muscles inserting in this area, and normal to the margin. The major and sometimes the only mantle margin retractor muscle in oysters originates as one source on the anterior curvature of the adductor muscle margin, at a slight indentation between the quick and catch parts of the latter, but it never leaves a scar on the shell's surface. A few similar but smaller ones may originate along the ventral and posterior margin of the adductor muscle in some species. From these origins large muscle bundles radiate and branch repeatedly before inserting on the mantle margin. These distinctive muscles have previously been undescribed and lacked a name; they are here termed the *pteriomorphic mantle margin retractor muscles,* because they also occur in some other monomyarian bivalves (Figure 3).

Secondary mantle margin retractor muscles (Figure 3) may originate at isolated spots in a line about at the level of the gill diaphragm, each extending as a single bundle or branching several times before inserting along the mantle margin. These occasionally leave an irregular, interrupted line of scars in the position of a pallial line on the shell (often prominent in *Saccostrea*).

The broad fusion of the mantle lobes to the left and right sides of the visceral mass is a factor of systematic importance. A lobe not so attached leaves a promyal passage between the anterior and posterior parts of the excurrent mantle chamber; this passage is morphologically supramyal, but the term "promyal passage" will be retained for it because of long established usage. A promyal passage may be present on left and right sides (*Hyotissa*), on the right side only (Crassostreinae, Pycnodonteinae except *Hyotissa*), or closed on both sides (Lophinae and Ostreinae).

The mantle lobes may be thin and transparent, in which case they are generally extensively papillate on their inner surfaces; in other species, the lobes are thick and opaque, used for food storage (glycogen), and papillation is local and rarely present. These extremes have intermediates (reduction of papillation and slight thickening of the lobes), and precise characterization for most species must await the study of more specimens than have been presently available.

In many oysters there is medial fusion of the two moieties, right and left, of the outer labial palp, forming a hood over the two branches of the inner palp, which never has such fusion (Figure 4). The amount of fusion varies among different species and is described under subordinate taxa.

In all oysters there are two gills, right and left, each with two demibranchs, medial and lateral; each demibranch consists of a descending and ascending lamella. The demibranchs are eulamellibranch (*i.e.,* with adjacent filaments of one lamella fused by tissue connections, leav-

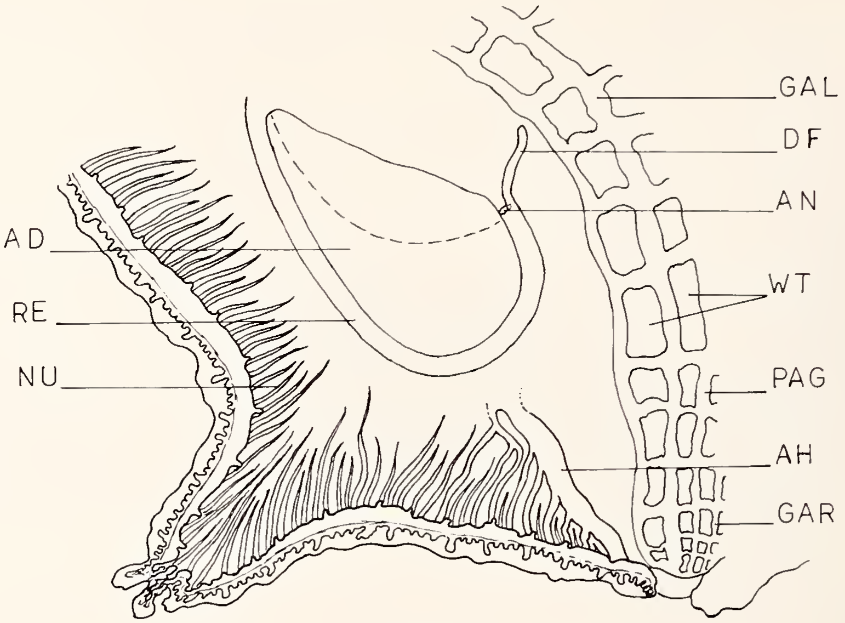

Figure 5

Internal view of posteroventral part of left mantle lobe of *Lopha cristagalli* from the New Hebrides Ids. (USNM 793723) to show anal appendage. Note extent of rectum around adductor muscle and tributaries to accessory heart. AD, adductor muscle; AN, anus; AH, accessory heart; DF, anal appendage; GAL, left gill axis; GAR, right gill axis; NU, neobranch unit; PAG, pseudoaxis of gill (fused junction of ascending lamellae of medial demibranchs); RE, rectum; WT, opening of water tubes of gill on surface of diaphragm.

ing small holes, or ostia, between them) and plicate (several small filaments of uniform size bulging outward to form a ridge between larger filaments in the grooves between the plicae), and all demibranchs are grooved along their free margin (Figure 4). There are regularly spaced, primary interlamellar septa extending from the free margin of each demibranch to the diaphragm; these septa define the water tubes, which are in oysters evenly coordinate in transverse rows in all four demibranchs. Thus they form a pattern of quadrate openings of the water tubes on the posterior (or excurrent) surface of the gill diaphragm (Figure 5). The gill diaphragm is completely attached by tissue continuity to the mantle lobes along the distal margins of the ascending lamellae of the lateral demibranchs. The diaphragm extends from the lower end of the labial palps to the inner surface of the post-ventral fusion of the mantle lobes, and thus the profile of the gills is J-shaped.

Along its dorsal half, the posterior surface of the diaphragm is attached to the anterior surface of the visceral mass by three narrow, non-muscular suspensory septa which are parallel to each other. The two lateral septa are attached along the gill axes, and they do not extend as far ventrad as the medial one, which is here termed the *pseudoaxial suspensory septum* (Figure 6). The latter resembles in all respects the axial septa, except in its extent and in attaching to the margins of the ascending lamellae of the inner demibranchs, which are here and lower down, beyond the septum, fused to each other by permanent tissue continuity. The pseudoaxial septum is a consequence of paedapody, and it is limited to the Ostreacea among living bivalves. It seems not to have been previously named or described.

In lateral view the three suspensory septa of the gills are elongate triangles, tapering to a point at the ventral ends of the labial palps (which surround the dorsal ends of the four demibranchs), and gradually widening to their terminations near the base (for the axial septa) or ventral end (for the pseudoaxial septum) of the metasoma (defined below). The ventral or free margins of all three septa are arched, being concave ventrally, and along this margin in the two gill axial septa, but not that of the pseudoaxial, there courses a prominent branchial nerve, originating from the visceral ganglia (see below). In most oysters the three septa are continuous sheets from the dorsal apices to the ventral free margins, but in at least two species—***Parahyotissa* (*Pliohyotissa*)** *quercinus* and *Striostrea prismatica*—the septa are discontinuous, being broken up into several segments (probably variable within a species) with large holes between, or the septa are entirely absent except for a short strip at their ventral ends, thus allowing passage of water between the three dorsal extensions of the anterior part of the excurrent mantle chamber which these three septa bound. The condition of discontinuous suspensory septa was only discovered late in my examination of oyster anatomies, and its presence in other species may have been overlooked.

The visceral mass extends as a short, tapering sac along the anterior curvature of the adductor muscle, to which it is attached; this projection is here termed the metasoma (Figure 6). It contains the distal end of the crystalline style sac (which opens throughout its length to the initial part of the intestine), allowing the long style to be straight, so that it can rotate on its axis.

The metasoma also contains an extension of the gonad, surrounding the style sac and intestine, and on its anterior surface open a pair of renopores and gonopores, medial to the cerebro-visceral connectives of the central nervous system. The position of the renopores relative to the tip of the metasoma differs at the family level.

After leaving the posteroventral part of the visceral mass the intestine, now termed the rectum, passes through the pericardium and along the posterior curve of the adductor muscle. Its extent across the ventral curve of this muscle before terminating at the anus varies at different taxonomic levels. Moreover, in most oysters there is an anal appendage attached to the anus (Figures 5, 8). The form of this appendage varies at different taxonomic levels.

There are no pedal ganglia or statocysts in post-larval oysters (a further consequence of paedapody). The visceral ganglia are flattened masses, fused to each other medially, located under the mantle epithelium on the anterior curvature of the adductor muscle, immediately ventrad of the distal end of the metasoma. From these ganglia radiate several pairs of nerves, the most prominent of which are the pair of branchial nerves cited above, the cerebro-visceral connectives, lateral to them, and the osphradial nerves, described below. A pair of small cerebral ganglia are by the mouth, attached to each other dorsally by a short commissure and each to a cerebro-visceral connective, but little attention was given to these ganglia in the present study.

A pair of sense organs, termed osphradia (possibly not homologous to the osphradia of other mollusks), is present on the ventral surface of the adductor muscle (Figure 6). Each is a low, transverse, semilunar lamella, projecting into the mantle cavity, extending medially from the margins of attachment of the muscle, and each osphradium is connected to the visceral ganglion on its side by a prominent osphradial nerve. The osphradia are usually white, even when the adjacent mantle is darkly colored; the right osphradium is always larger than the left, and situated closer to the anus than the left one, regardless of the extent of the rectum around the ventral curvature of the adductor muscle.

Thiele (1889) first described these "abdominal sense organs," noting their presence in species of *Arca, Glycymeris, Pteria, Pinctada, Pinna, Pecten, Lima,* and *Spondylus* (some of his generic names are here modernized), as well as in *Ostrea edulis.* He could not find the organs in the Mytilidae, the protobranchs of the genera *Nucula* and *Nuculana,* nor any siphonate bivalves. He did not find the minute left organ in *O. edulis,* but his figure (*loc. cit.,* fig. 9) shows very well the cardiform shape of the anal appendage of this species, although he did not mention it in the text.

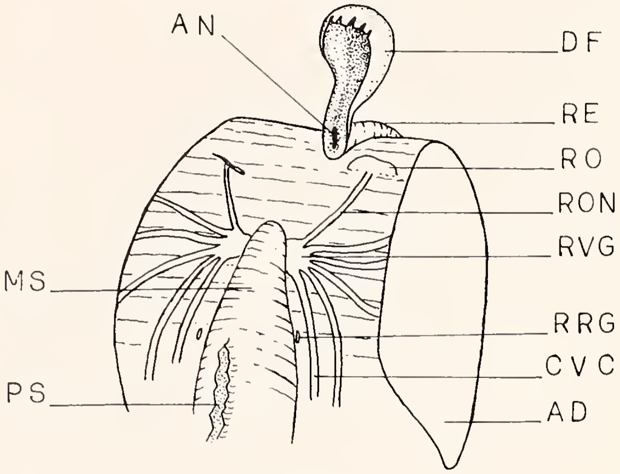

Figure 6

Oblique view of anteroventral curve of the free surface of the adductor muscle of a specimen of *Dendostrea folium,* 22 mm high, from Port Victoria, Seychelles Ids. (USNM 778093). AD, adductor muscle; AN, anus; CVC, cerebro-visceral connective; DF, anal appendage; MS, metasoma; PS, pseudoaxial suspensory septum of gills (cut); RE, rectum; RO, right osphradium; RON, right osphradial nerve; RRG, right reno-gonopore; RVG, right visceral ganglion.

The right and left parts of the heart are brought together in front of the rectum, and the auricles are always fused to each other, so that their cavities communicate, but they separate before entering independently into the single, bilobed ventricle (Figure 9). Variation within the heart, and its relation to the rectum and kidney are explained below, at the family level.

Based on studies of a few species of the Ostreidae, oysters have long been known to be hermaphroditic. But members of that family are sequential hermaphrodites, *i.e.,* they produce both sperm and ova in the same follicles of a single pair of gonads, but at different seasons. At least some of the Gryphaeidae are concurrent hermaphrodites, having a pair of testes and a pair of ovaries present together in the same individual.

Nothing is known of the reproductive habits of the living Gryphaeidae; of the Ostreidae, the Crassostreinae that have been studied are oviparous, shedding the gametes into the sea, where fertilization and development occur. The Lophinae and Ostreinae both seem to be larviparous, retaining the fertilized ova in the mantle cavity until the larvae have shells and can swim. Those two subfamilies are unique among incubating bivalves, in that the larvae occur only in the incurrent mantle cavity, nearly filling it and the area around the labial palps (at least in preserved specimens). Little emphasis has been given to this unusual

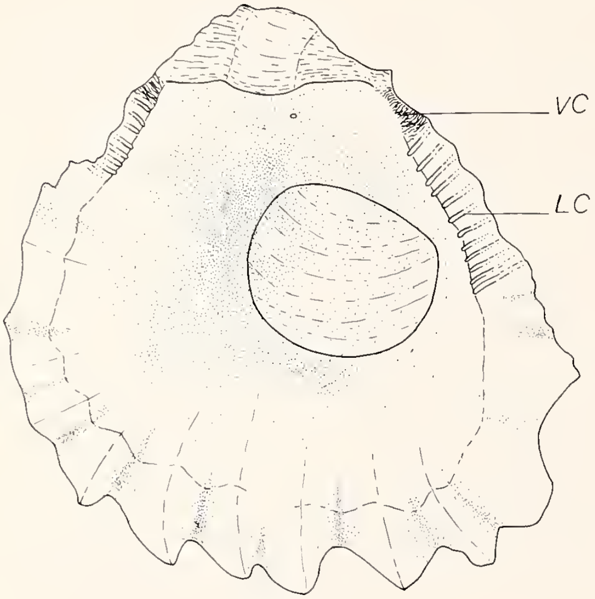

Figure 7

Hyotissa hyotis. Interior of a right valve, 180 mm high, showing lath chomata (LC) below vermiculate chomata (VC). From Okinawa, Ryukyu Ids. (USNM 670956).

condition, and the hypothetical explanations of how the gametes (or zygotes?) attain the incurrent chamber when they are released in the excurrent one are not convincing (see GALTSOFF, 1964).

All Ostreacea are marine, occurring from tropical to cool temperate seas, but they are most diversified in warmer areas. None occurs in the Arctic or Antarctic zones. There is considerable variation in the preferred range of salinity, temperature, water turbulence, substrate type, and depth for different species.

Family GRYPHAEIDAE Vyalov, 1936

Ostreacea in which the adductor muscle scars are circular or only slightly flattened dorsally.

Two of the three subfamilies, the Gryphaeinae and Exogyrinae, are extinct; they were reviewed by STENZEL (1971) and briefly redefined by HARRY & DOCKERY (1983). All living gryphaeid oysters belong to a single subfamily, as follows.

Subfamily PYCNODONTEINAE Stenzel, 1959

Gryphaeidae in which the chalky deposits interspersed in the foliar matter of the inner shell layer have vesicles (hollow, subspherical or polyhedral cavities) easily seen with magnification of 10× or more. This is termed vesicular shell structure; it is well illustrated in RANSON (1967), STENZEL (1971), and TORIGOE (1981). The inner edge of the commissural shelf, along the shell margin, is usually well defined by a prominent angle of the shell surface.

Chomata are always present. These are of three types in this subfamily: (1) *Vermiculate chomata* (Figure 7) are small, rounded ridges, closely spaced, normal to the margin; they are slightly twisted, tapering out so that they are of varied lengths, or dividing and fusing. They are always present near the ligament on the front and hind margins of both valves, but those of opposite valves do not interdigitate. Usually the surface on which they occur is flat, but it may be creased to various degrees in the left valve, parallel to the margin, with a corresponding ridge in the right valve, fitting into the crease. When well manifest, these will be referred to as the chomatal troughs and ridges. (2) The *neopycnodontine chomata* are modifications of the vermiculate type, having very pronounced ridges and troughs, with the vermiculate chomata greatly enlarged as they cross the crests of the ridges on the right valve (Figure 16, but the ridges and troughs are not well shown); there are pits to receive the individual enlargements in the chomatal troughs of the left valve. This type is also limited to the shell margin near the ligament. It is intermediate between the vermiculate and ostreine types (see below, under Ostreidae) of chomata. (3) *Lath chomata* (Figure 7) are elongate, straight, well defined ridges, spaced about as far apart as their widths, and normal to the margin. They occur ventral to the vermiculate chomata, on both right and left valves, but they seem to coincide rather than interlock, or alternate, with those of the opposite valve. These are present only in some specimens of *Hyotissa hyotis,* among living oysters.

The mantle lobes are thin, transparent in smaller specimens, and probably not used to store glycogen; their inner surface is usually extensively papillate, becoming more densely so in older individuals. The first neobranch unit behind the diaphragm is not expanded nor extended inward to form an accessory heart. The outer labial palp is fused medially for most of its length. The anus is surrounded by a fleshy, collarlike flange, often rolled outward to appear as a bulbous mass in preserved specimens (Figure 8). The right promyal passage is broadly open, reaching from the adductory muscle nearly to the isthmian mantle.

The bilobed ventricle of the heart is distinctly penetrated by the rectum. The auricles of the heart are fused to each other, and also extensively adnate to the ventral wall of the pericardium, over the adductor muscle; they are irregularly outpocketed, appearing lobate (Figure 9); internally they are packed with granulocytes containing a dark brown, granular pigment, but a central, tubular lumen persists in each auricle for passage of blood to the ventricle. The renopericardial passage, if present, has not been located.

The granulocytes in the auricles of bivalves were extensively treated by GROBBEN (1888), who thought they are excretory cells. These cells are less abundant in those species of Ostreidae in which they occur (*e.g., Ostrea edulis*), but insufficient observations were made on the his-

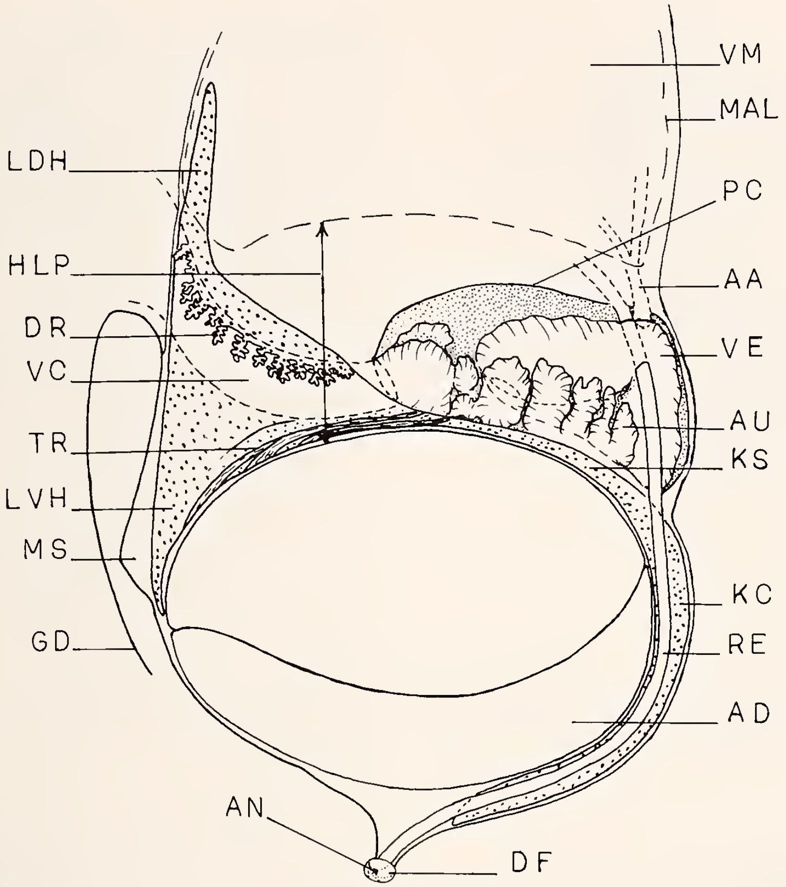

Figure 8

Reno-pericardial complex of *Hyotissa hyotis,* viewed from the left side and showing the left promyal passage which is unique to this species. Based on a specimen from the Galapagos Ids. (USNM 796193). AA, anterior aorta (posterior not shown); AD, adductor muscle; AN, anus; AU, auricle of heart; DF, anal appendage; DR, dendritic intrusions of kidney between left vena cava and mantle; GD, gill diaphragm; HLP, height of left promyal passage; KC, kidney caecum; KS, main kidney sac; LDH, left dorsal horn of kidney; LVH, left ventral horn of kidney; MAL, limit of attachment of left mantle lobe to visceral mass; MS, metasoma; PC, pericardium; RE, rectum; TR, trabecular strand in kidney sac; VC, left vena cava (blood passage from left side of body to left auricle); VE, ventricle of heart; VM, visceral mass.

tology of the heart auricles of the Ostreidae to include them in this paper. WHITE (1942) greatly extended Grobben's survey of these granulocytes in bivalves, but provided scant data on oysters.

The kidney (Figure 8) is a large, flattened, thin-walled sac with several extensions. The major part of it is central, covering the whole dorsal surface of the adductor muscle between the latter and the pericardium. From the central part there extends a long, cylindrical caecum around the posterior curvature of the muscle; this is on the right side of the rectum, which it resembles in size. But it has a thinner wall, and it ends abruptly at the posteroventral curve of the muscle, apparently without an opening there. From the anterior end of the central sac there are two extensions, right and left, each forming a large sac beside the metasoma. Each of these anterior horns, as they will be called, extends ventrally and dorsally from their junction with the central sac. The renopores are near the dorsal ends of these horns. The central sac has within it a few long, transverse trabeculae passing from the lower to the upper surface, and completely free from either wall except where they attach at their ends. These may branch a few times.

A pair of lateral branches of the kidney sac intrude between the mantle and the large venous sinuses leading from the gill diaphragm to the heart auricles. These have a few small, dendritically branched outpocketings, or alveoli, but such are absent elsewhere in the kidney of oysters of this subfamily.

The interlamellar partitions of the gill demibranchs are

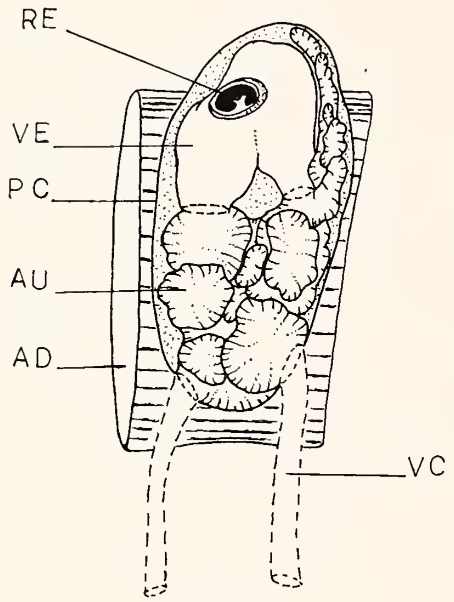

Figure 9

Dorsal view of heart of *Hyotissa hyotis* from Galapagos Ids. (USNM 796193). Note the many lobes of the auricles; the thin walled kidney, between the pericardium and adductor muscle, is not shown. AD, adductor muscle; AU, auricle of heart; PC, pericardium; RE, rectum; VC, left vena cava; VE, ventricle of heart.

very wide, so that the gills appear to be more voluminous than those of the Ostreidae.

When alive, the species that grow to large size, at least, have brilliant orange pigment in the gonad (ovary) and adductor muscle. The pigment may be seasonal and it is alcohol soluble, so that it is not apparent in the flesh of most preserved specimens. Specimens preserved in alcohol usually have a dark brown pigment in the parenchyma, which is more abundant in older (larger) oysters.

Tribe **Hyotissini** Harry, new tribe

Pycnodonteinae in which the shells are thin to thick, small to very large, with vermiculate chomata always present near the hinge. The interior of the valves have a moiré luster; the right valve is often inflated to a variable extent. The prismatic layer of the right valve is thin, frequently lost through erosion. Tuck grooves (see next tribe) on the right valve are rare. These generally live in shallower depths than the Neopycnodontini. The condition of the promyal passages varies at the generic level.

Genus *Hyotissa* Stenzel, 1971

Type, by original designation: *Mytilus hyotis* Linné, 1758, Syst. Nat., Ed. 10, p. 704, No. 270. See Figures 7, 10 and 11; also STENZEL (1971) fig. J85, p. N1111.

Hyotissini with medium to very large shells (to 250 mm height or more), occasionally subcircular but usually oval, dorsoventrally elongate; both of the valves are thick, and both usually have rounded plications, from which semicylindrical lamellae may project as hyote spines. The marginal commissure is usually zigzag, with vesicular chalky deposits developing internally in the troughs between the plicae. The ventral margin of the adductor muscle scar is usually elevated, at least in larger shells. Lath chomata (Figure 7) occasionally develop. The valves are variously colored, washed with red, blue, or purple. Some specimens are light brown externally, and occasionally specimens will have dark purple, almost black margins internally, or the whole inner surface may be so colored.

The left promyal passage is open, but limited to the area of the pericardium and lower part of the visceral mass (Figure 8); it is thus not as extensive as the right passage, which extends from the adductor muscle nearly to the hinge. In larger specimens the papillate inner surface of the mantle is rough to the touch.

As here restricted, the genus is monotypic, but *Hyotissa hyotis* extends from Madagascar to the Tuamotu Islands in the Indo-West Pacific tropics, and it also occurs in the tropical part of the eastern Pacific faunal realm. It lives in shallow subtidal depths, often on coral reefs. Junior synonyms of the population of the eastern Pacific include *Ostrea fischeri* Dall, 1914. There are numerous junior synonyms of the Indo-West Pacific population.

Genus ***Parahyotissa*** Harry, gen. nov.

Type: *Ostrea thomasi* McLean, 1941, Notulae Naturae (Acad. Nat. Sci. Philadelphia), No. 67, p. 7, pl. 3, figs. 1, 2; pl. 4, figs. 1, 2. Not *Ostrea sellaeformis* var. *thomasii* "Conrad" Glenn, 1904, Maryland Geol. Surv., Miocene, p. 380, pl. C, figs. 5a, 5b. McLean's species is here renamed ***Parahyotissa*** *mcgintyi* to preserve his original intention to honor Thomas L. McGinty, noted student of malacology of Florida. See Figures 12 and 13; also STENZEL (1971) fig. J27, p. N987.

Hyotissini in which the shell is smaller than *Hyotissa,* without lath chomata, but with vermiculate chomata always present and restricted to the subligamental margin. The ventral margin of the muscle scar is not elevated. Plications, occasionally with short hyote spines, are potentially present on both valves. The valves are often washed with red or light purple, tending to be white inside. In contrast to *Hyotissa,* the left promyal passage is always closed.

Parahyotissa (***Parahyotissa***) *mcgintyi* occurs subtidally and to 98 m depth or slightly more in the tropical eastern and western Atlantic Ocean, extending slightly into subtropical areas in the latter realm (to North Carolina and Texas). Another species of the typical subgenus, ***P.*** (***Parahyotissa***) *imbricata* (Lamarck, 1819), occurs in the central part of the Indo-West Pacific tropics (Australia to the Ryukyu Islands of Japan); its shells may be difficult to distinguish from juveniles of *H. hyotis,* but the left promyal passage is closed.

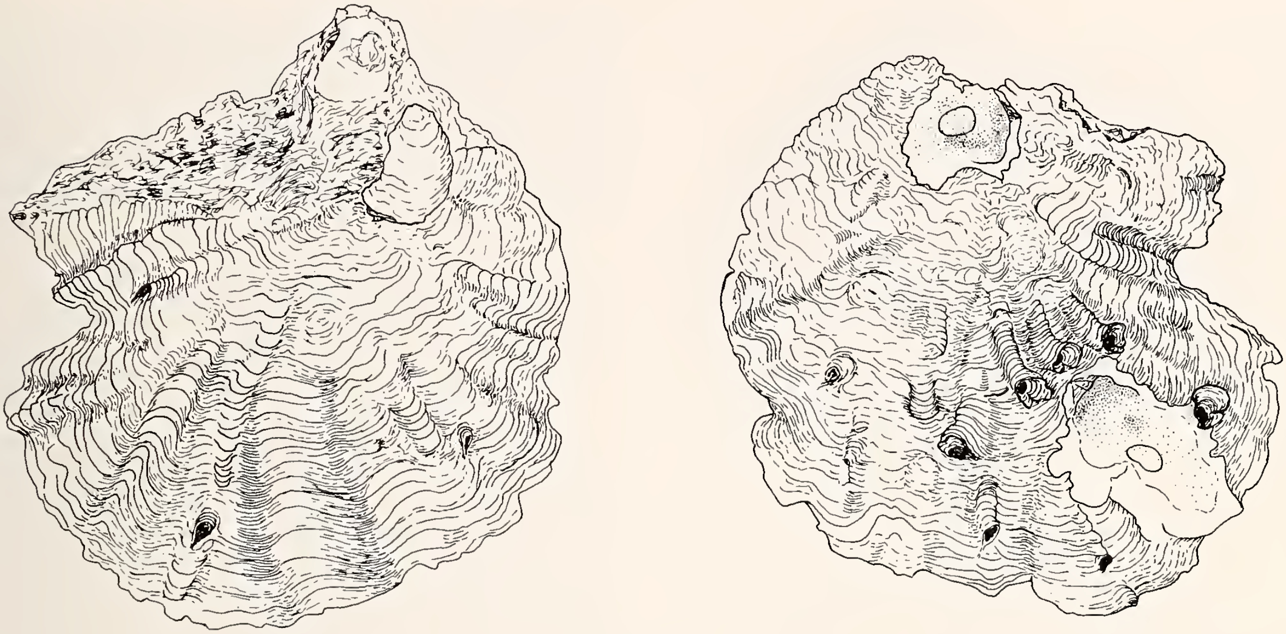

Figure 10

Hyotissa hyotis. Exterior of valves (left one on left), 130 mm high. Galapagos Ids. (USNM 796193).

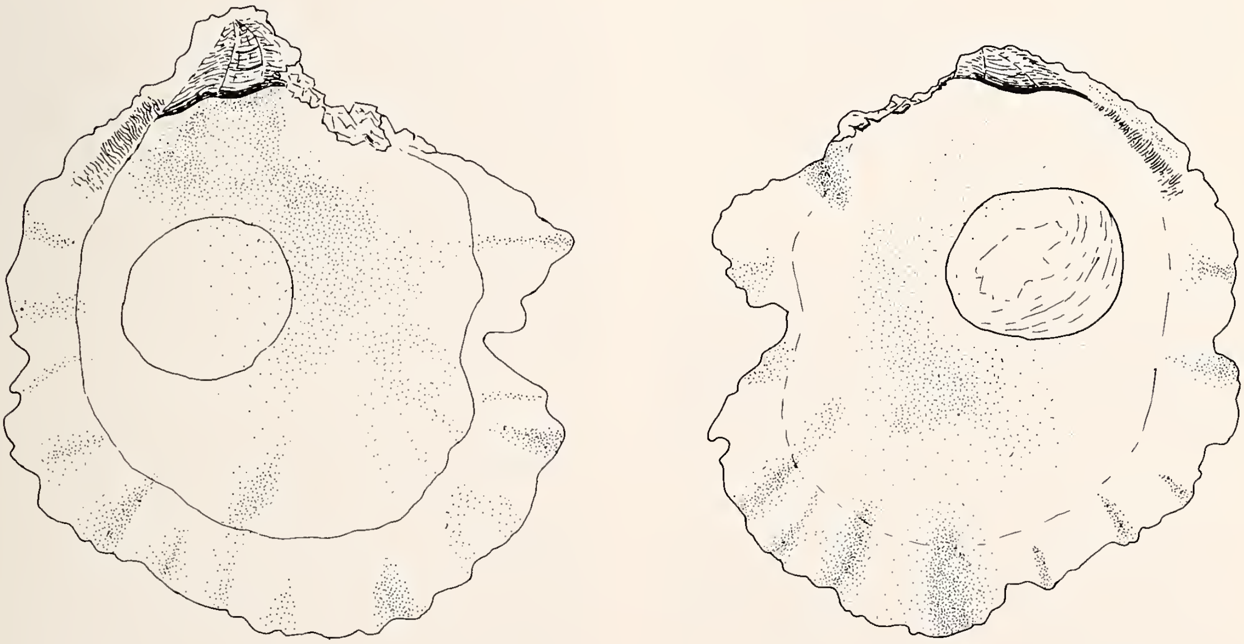

Figure 11

Hyotissa hyotis. Interior of valves of shell of Figure 10.

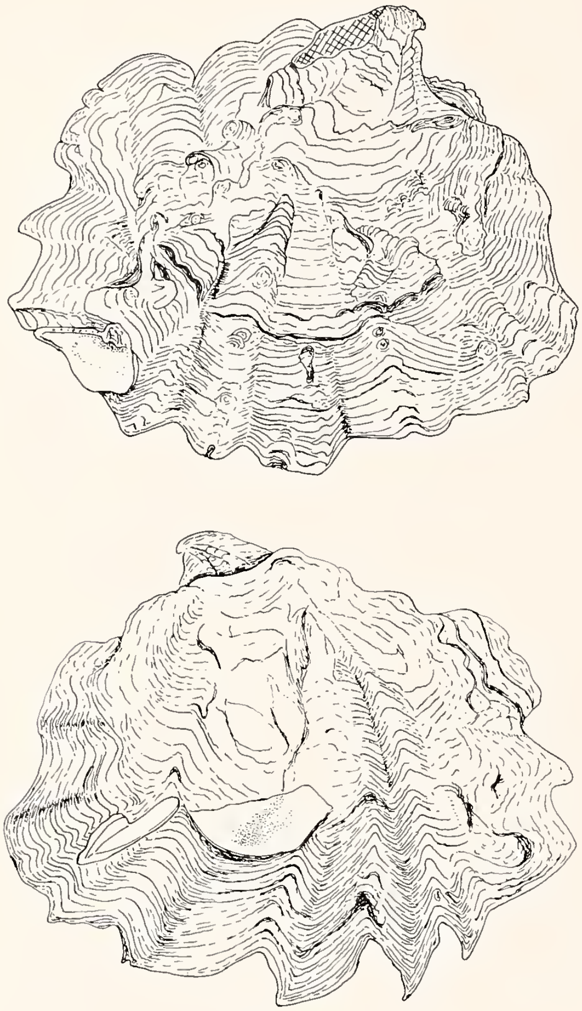

Figure 12

Parahyotissa *mcgintyi*. Exterior of left (above) and right valves of a specimen 65 mm long, from several meters depth on a support of an oil drilling platform, several kilometers south of Timbalier Island, Louisiana. Shell loaned by C. A. Beddinger. Small attachment area of left valve, cross hatched, only partly visible.

Subgenus ***Parahyotissa*** (***Pliohyotissa***)
Harry, subgen. nov.

Type: *Ostraea quercinus* Sowerby, 1871, *in Ostraea* of Reeve's Conch. Icon., 18, pl. 19, figs. 43a, 43b. See Figure 14.

Pliohyotissa differs from the typical subgenus in the nearly complete absence of plications and spines on the valves, which otherwise grow to a size comparable to that of ***Parahyotissa*** *s.s.,* by the oaken color (irregular light brown wash) of the shell's interior (which may occur in the typical subgenus also), and by the frequent presence of narrow, marginal rays of purple. ***Parahyotissa*** (***Pliohyotissa***) *quercinus* (Sowerby, 1871) was originally described from unknown locality. It lives in the eastern Pacific, particularly along the east coast of Baja California, where it was rediscovered by Constance E. Boone. The holotype of Sowerby's species in the British Museum of Natural History has a few small plicae on the slightly upturned margin of the left valve, but the marginal commissure is not zigzag. As presently known, this subgenus is monotypic.

Subgenus ***Parahyotissa*** (***Numismoida***)
Harry, subgen. nov.

Type: *Ostrea numisma* Lamarck, 1918, Hist. Nat. Anim. sans Vert., Vol. 6, pt. 1, p. 205, No. 8. Not figured. See Figure 15.

Parahyotissa in which the shell is small (40 mm high or usually less), extensively cemented by the left valve; the right valve is slightly convex, without plicae or spines; it is usually white, occasionally with a few small purple spots near the umbo. The only known species, ***P.*** (***Numismoida***) *numisma* (Lamarck, 1819) is widely distributed in the Indo-West Pacific tropics from East Africa to Hawaii and the Tuamotu Islands. Junior synonyms include *Ostrea thaanumi* Dall, Bartsch & Rehder, 1938, of Hawaii.

Tribe **Neopycnodontini** Harry, new tribe

Pycnodonteinae in which the shells are thin and of small to moderate size, with the left valve very inflated and right valve flat. The chomata are of the neopycnodonteine type. The right valve has a few peculiar linear, radiating grooves, each margined by a small ridge near the shell margin of larger specimens, resembling tucks in a piece of cloth. The left valve rarely shows a few plications (large, vague, discontinuous) but none are present on the right valve. The shells are generally light gray, occasionally washed with light pink or lavender. The interior surface of the shell does not have moiré luster. The left promyal passage is always closed; the right one is broadly open.

Genus *Neopycnodonte* Stenzel, 1971

Type, by original designation: *Ostrea cochlear* Poli, 1795. Testacea utriusque Siliciae, Vol. 2, p. 179. See Figure 16.

The single species of this genus, *Neopycnodonte cochlear* (Poli, 1795), is nearly circumglobal in lower latitudes. Although some specimens of ***Parahyotissa*** may extend to the shallower limit of depth of *N. cochlear,* this species extends to greater depths than any other Recent oyster: 27 to 2100 m; but the populations seem to be very localized throughout its range. It has been abundantly recorded in the eastern Atlantic from the Mediterranean and Atlantic coasts of France; the U.S. National Museum of Natural History has much material from the western Atlantic, from Bermuda, North Carolina, and the east coast of Florida, and I have a specimen found off south Texas (27°18′N, 96°23′W, 131 m depth). In the Indo-West Pacific realm it is represented in the USNM by specimens from the Red Sea to Madagascar, the Philippines, China Sea, Japan and Hawaii. The species is unknown from the eastern Pacific faunal realm. There are numerous junior synonyms.

Family OSTREIDAE Rafinesque, 1815

Ostreacea in which the dorsal margin of the adductor muscle scar is concave or flat, so that the shape of the scar is gibbous, or more frequently reniform or lacrimoid. The valves generally lack moiré luster internally. Chalky deposits of the foliar layer, when present, do not show vesicles at lower magnification, although at high magnification these deposits may be seen to be minutely vesicular (CARRIKER *et al.,* 1980). A marginal commissural shelf is generally not defined (exception: ***Planostrea***).

Chomata may be absent throughout life (***Booneostrea,*** *Crassostrea*) or occasionally lost in larger (older) shells of some species (*Ostrea, Striostrea,* ***Pustulostrea***), or absent in some ecomorphs of a species in which they are generally present (*Saccostrea*); but chomata are present in most species, and of two distinct types: (1) *Lophine chomata,* limited to the Tribe **Lophini**, consist of minute pustules in adjacent lines which are normal to the shell margin, with one to several pustules per line. The lines of pustules are on the protochomatal bands usually manifest in the underlying shell structure. Lophine chomata may form a broad, continuous band completely around the shell margin, or occur only at a few places along it; the pattern may change drastically within the life of an individual. They may be present on both valves, or limited to the right valve only, but in either case there are no pits to receive them in the opposite valve. Occasionally lophine and ostreine chomata may occur in the same specimen (*Dendostrea, Alectryonella*), in which case the ostreine chomata are limited to the margin close to the hinge. (2) *Ostreine chomata* consist of pustules, sometimes elongate normal to the shell margin, in a single line parallel to the shell margin; they occur only on the right valve, and there are pits to receive them in the left one. Ostreine chomata may be only a few, in which case they are usually near the ligament, or they may extend ventrally for variable distances, sometimes to or even across the ventral margin. Only this type of chomata is present in the tribe **Myrakeenini** of the Lophinae, and in the Ostreinae and Crassostreinae (with exceptions noted above).

The left promyal passage is always closed; the right one is closed in Lophinae and Ostreinae, but partially open in the Crassostreinae. The first neobranch unit behind the diaphragm usually is enlarged and extends inward (upward) to form an accessory heart. The rectum passes completely behind the ventricle of the heart rather than through it. The heart auricles are not outpocketed, nor are they adnate to the ventral wall of the pericardium. Generally parenchyma and pigmented granulocytes are sparse in the heart auricles.

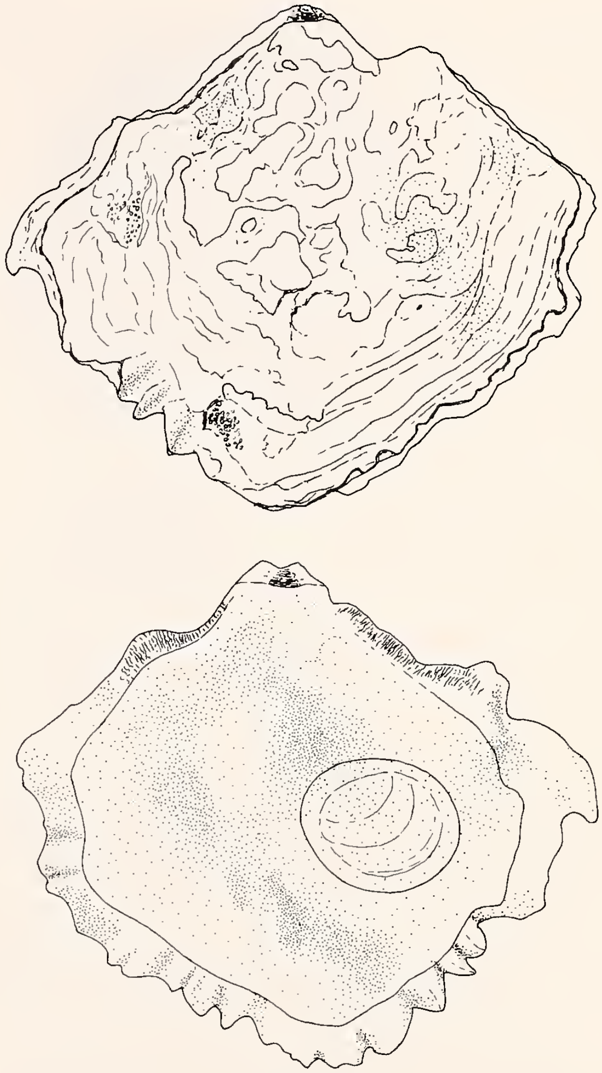

Figure 13

Parahyotissa *mcgintyi.* Shell 89 mm long. Exterior of right valve (above) with margin of left showing, and interior of same below. Note extreme erosion and poorly developed plicae; left valve was almost entirely cemented to bedrock. Shell is from Stetson's Reef, near the edge of the continental shelf, off the northern Texas coast; collected and loaned by Thomas E. Pulley.

The main sac of the kidney of the Gryphaeidae is reduced to a small, transverse tube at the anterior curve of the adductor muscle, between it and the front end of the pericardium; there are no posterior kidney caecum or internal trabeculae; the anterior horns of the kidney are present, lateral to the metasoma, and these extend above and below the transverse tube. A large lateral tube is often present, extending backward from the anterior horns lateral to the dorsal part of the pericardium. All these tubes

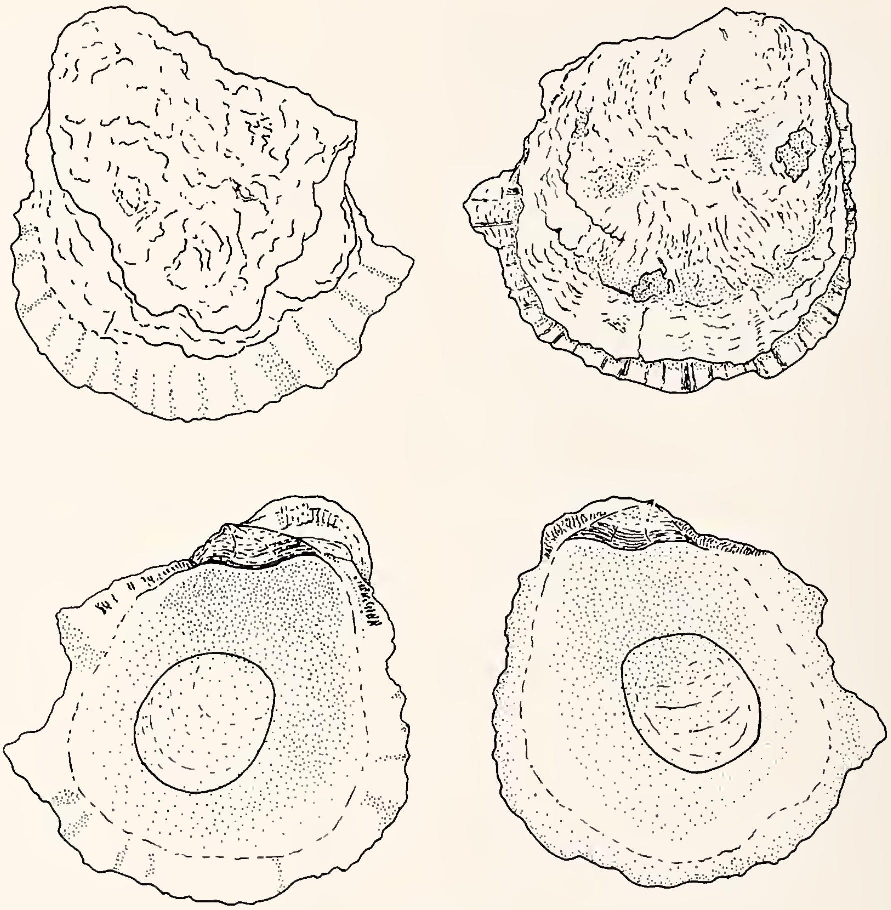

Figure 14

***Parahyotissa* (*Pliohyotissa*)** *quercinus.* Height, 65 mm. Concepción, Baja California Sur, Mexico, low intertidal zone. Shell collected and loaned by Constance E. Boone.

are obscured because they have arising from them short, closely spaced, dendritically branched follicles, and the whole kidney mass is often nearly colorless, or sometimes pure white.

The reno-pericardial passage consists of two large openings between the pericardium and the transverse kidney tube. These openings are just above the lateral ends of the auricles. The renopores are at the lower ends of the anterior kidney horns, and they open with the gonopores in small pits, lateral to the free end of the metasoma (Figure 6).

Subfamily Lophinae Vyalov, 1936

Ostreidae of small to large size, usually with plicate surfaces on both valves and generally having a zigzag marginal commissure. The area of cementation of the left valve may be large, but it is usually small and often accompanied by thin, recurved hyote spines which may be of considerable length or mere rudiments, often free throughout their length and only attached to a solid object terminally; these clasper, or lophine, spines arise at the crests of plications of the left valve only, and at or close to the outer margin of the area of cementation. The outer (prismatic) layer of the shell is usually continuous, not projecting as lamellae at growth rests.

The interior of the shell often has a metallic luster, and frequently it is of some color other than white (brown, greenish, or reddish). The adductor muscle scars are generally not colored differently from the rest of the shell's interior. Chalk deposits are absent (as noted also by Torigoe, 1981), but shell chambering is frequent. Chomata are always present, either lophine or ostreine or both.

The mantle lobes are usually thin (exception: ***Myrakeena***) and occasionally their inner surfaces are papillate. Both promyal passages are closed. The outer labial palp is fused medially, usually for the greater part of its length. The rectum extends well under the adductor muscle, sometimes curving upward around the anterior part of the

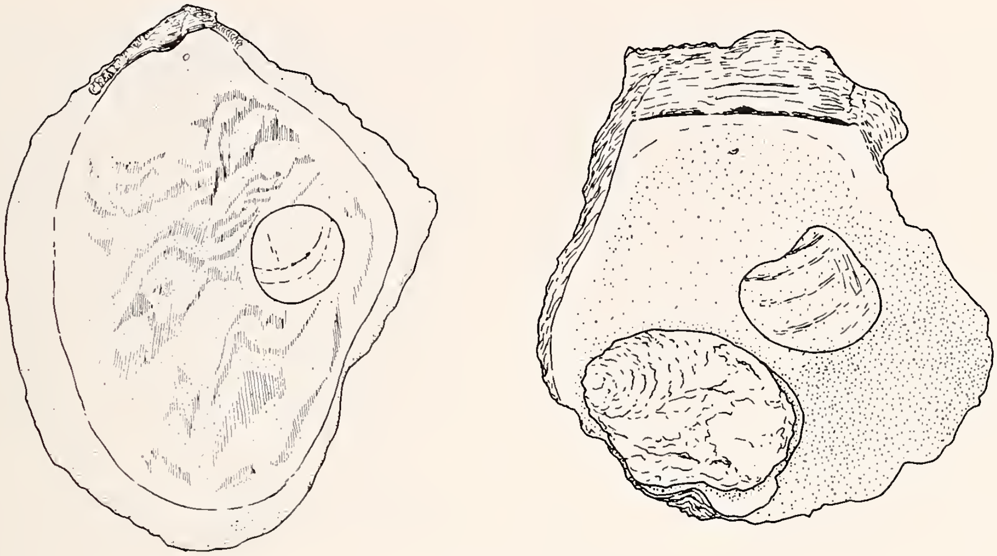

Figure 15

Parahyotissa* (*Numismoida*)** *numisma.* Right: exterior of right valve, attached to left valve, the latter cemented completely by its outer surface to the inner surface (near ventral margin) of a slightly worn right valve of ***Pustulostrea *tuberculata.* Left: interior of same right valve, showing moiré luster. The ***P.*** (*N.*) *numisma* shell is 28 mm high. From Efate Island, New Hebrides Ids. (USNM 787771).

muscle for a short distance. The anus has a large, digitiform process extending from the outer part of its rim (Figure 5).

The gonad may be brightly colored (yellow) seasonally by a pigment that quickly leaches out in alcohol. The species are larviparous (where reproductive habits are known).

Lophine oysters live in tropical or warm temperate marine waters from shallow subtidal levels to a few meters depth, generally in situations where they are not subject to turbulence and where the water is of constant temperature and normal oceanic salinity. Several species are typically coral reef associates.

The Lophinae show their close relationship to the Pycnodonteinae in several characters that are lost or much modified in the rest of the Ostreidae; thus, both valves are usually strongly plicate (lost in some species of both subfamilies); the outer labial palp is more extensively fused medially than in the rest of the Ostreidae; mantle lobes are usually thin and papillate on the inner surface. They are more strictly limited to the tropics than the other living oysters, and are primarily coral reef associates. Conversely, new characters appear in the Lophinae which are also present in the Ostreinae but not in the Pycnodonteinae: ostreine chomata; a digitiform anal appendage; a closed right promyal passage and habit of brooding the larvae; modification of the first neobranch unit behind the gill diaphragm to become an accessory heart; and a tendency in some (***Myrakeena***) to loose the papillation of the inner surface of the mantle lobes and to thicken them for storing glycogen. TORIGOE (1981:pls. 1–5) illustrated and described a pattern of the intestine within the visceral mass in which the intestine does not loop around the stomach in the Pycnodonteinae and Lophinae, but does do so in the Ostreinae and Crassostreinae; but I have made no observations on this point.

Tribe **Lophini** Vyalov, 1936, new tribe

Nom. trans. Harry, herein, *ex* Lophinae Vyalov, 1936.

Lophinae in which only lophine chomata occur (*Lopha*), or both lophine and ostreine types may occur, together or separately (*Alectryonella, Dendostrea*). Clasper spines may arise from the left valve, but these are often reduced or absent. Although the species may have completely white shells, the shells are usually deeply colored, red, brown, blue, or purple (or combinations thereof), either by washes or by prominent radial stripes or both. There is no circular flange around the anus, which has a prominent digitiform appendage on its outer margin.

Genus *Lopha* Röding, 1798

Type, by subsequent designation of Dall (1898): *Mytilus cristagalli* Linné, 1758, Syst. Nat., Ed. 10, p. 704. STENZEL (1971) figured this species, fig. J129, p. N1156, under the name "*Lopha folium* ecomorph *cristagalli.*"

Lophini in which the shell becomes large (to 100 mm high) and is subcircular to oval-reniform in profile, with about five very large, interlocking, radial plicae on both

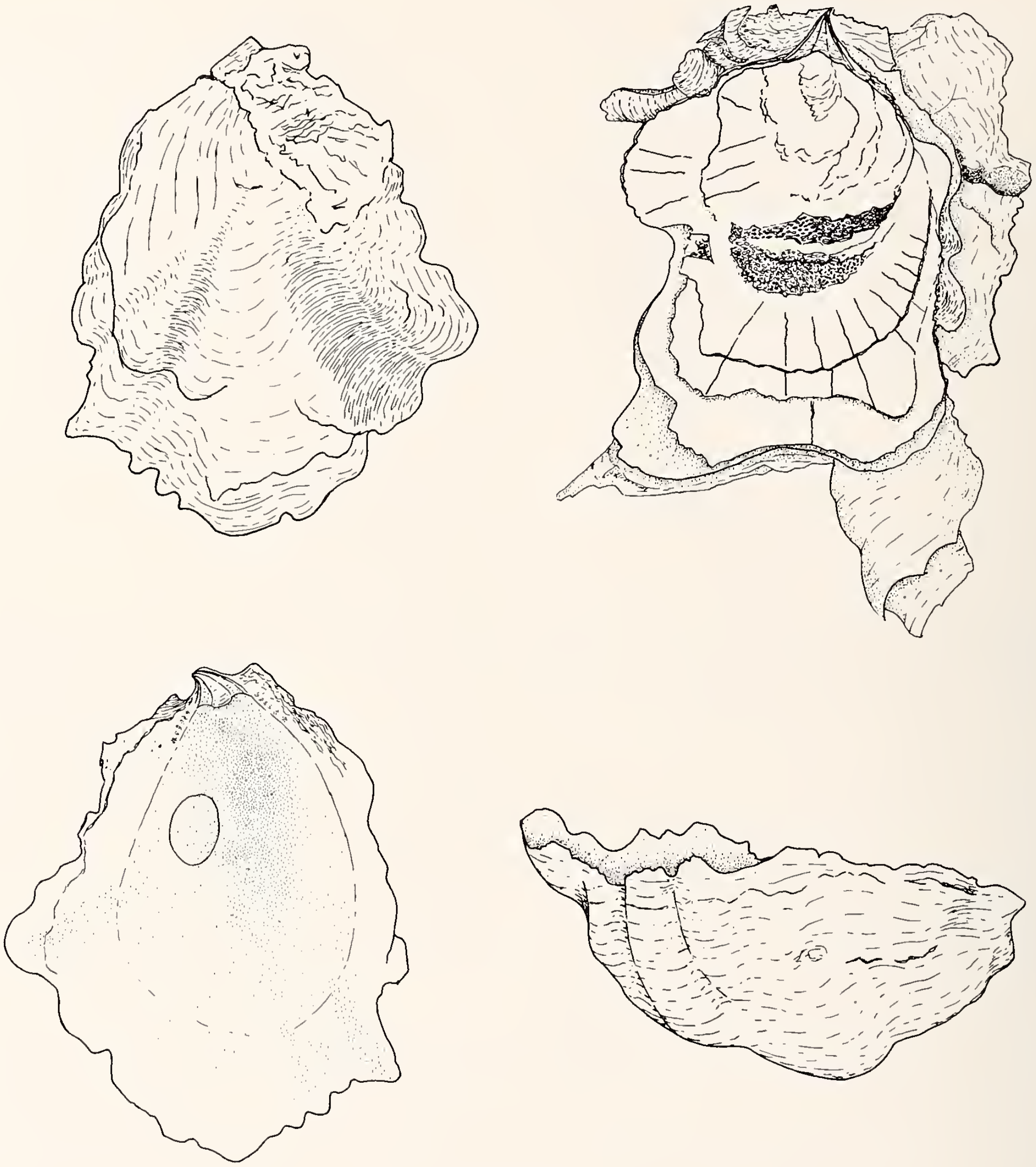

Figure 16

Neopycnodonte cochlear. Upper right: exterior of right valve, still attached to left valve (54 mm high), which is cemented to a cluster of other specimens. Note crescent-shaped abraded areas in middle of valve, revealing vesicular chalk deposits, and radial "tuck marks" peripherally. Specimen is one of lot USNM 196421, from Sicily, part of the Jeffreys Collection. The other three figures are of a left valve, 63 mm high, one of lot USNM 249152, from 270 m depth in the China Sea, off Pratas Island (116°40′E, 20°40′N).

valves; the ridges and troughs of these plications are acutely angled, and the sides flattened. There are nearly always some low, rounded or quadrate pustules, very small, arranged in radial rows, covering the surface of both valves or present only in limited areas. These are smaller than the pustules of *Alectryonella* and ***Pustulostrea.*** The area of cementation is generally small; clasper spines are usually present, and they are often long (to several cm) and irregularly recurved. The right valve usually has externally a distinct indentation over each spine of the left valve.

The shells are thin, with the inner surface usually metallic, bronzed or rarely white. No chalk deposits seem to form, but chambering is used to smooth the interior and eliminate the plications inward from the narrow marginal zone. Chomata are lophine only; they are prominent, often extending to and around the ventral margin; they are present in both valves or the right valve only.

Mantle lobes of the two alcoholic specimens examined (from the New Hebrides Ids., USNM 793723) are thin, transparent, and papillate on their inner surfaces. The first neobranch unit behind the diaphragm is enlarged and receives as tributaries the next two or three units above it (Figure 5). The outer labial palp is fused in the midline almost to its tip. The rectum passes ventrally under the adductor muscle and ends on the anterior curvature; the anus has a very large, flattened, fingerlike appendage, narrow and tapering to an acute tip, arising from the outer curve of the lip (Figure 5). Both promyal passages are closed.

STENZEL (1971:N1005) cites WADA (1953, a paper not available to me) as saying this species and the next (*Alectryonella plicatula*) incubate their larvae.

The genus is here considered to be monotypic, and the two other species that STENZEL (1971) included as synonyms are placed in *Dendostrea*. TORIGOE (1981) reached the same conclusion. As thus restricted, *Lopha cristagalli* is limited to the tropics of the Indo-West Pacific faunal realm, associated with coral reefs at a few meters depth; it extends from the east coast of Africa and the Red Sea to the Ryukyu Islands of Japan, and to 165°E longitude. While it is not uncommon in the Philippines and Indonesia, it seems to be rare in the waters of northern Australia. Junior synonyms include *Ostrea townsendi* Melvill, 1898, and the two specimens on which this name was based were examined in the British Museum; both are white, inside and out, but one is faintly washed with pale pink and the other with pale lavender on the exterior near the umbos.

Genus *Alectryonella* Sacco, 1897

Type, by original designation: *Ostrea plicatula* Gmelin, 1791, Syst. Nat., Ed. 13, p. 3336, No. 111. See STENZEL (1971) concerning the interpretation of Gmelin's species, and for excellent photographs of it: fig. J29, p. N990; J134, p. N161; J135, p. N1162.

Lophini with shells of moderate size (but to 110 mm long), subcircular, slightly inflated, usually cemented by about half of the left valve. Clasper spines are rarely formed, and usually they are short and adnate throughout their length. Numerous (up to 20) regular, rounded radial ribs are present on both valves. These plications are roughened by closely spaced growth rests, but no lamellae seem to be formed along them. Low, rounded pustules, closely spaced and irregularly arranged, may occur on adumbonal parts of the shell before the plications are formed; these are larger than those of *Lopha*, and they resemble those of ***Pustulostrea*** (see below). The beaks are moderately large, and the ligament is short to long. The exterior is usually dark bluish purple or brown, uniformly colored.

The interior is often dark brown, submetallic. No chalk deposits are formed, but chambering is common in the deeper parts of the left valve, at least. Chomata may be ostreine near the hinge, but typically lophine on the rest of the shell margin, where they are often prominent on both valves, or the right one only.

Protochomatal bands are manifest in small patches by narrow, thin strips of brown, organic material (conchiolin) deposited at any place on the shell interior (rare on the muscle scars); these bands are closely spaced, mostly parallel to each other and chiefly normal to the shell margin, especially near it, but inward they may become whorled and branched, forming a pattern similar to a human fingerprint. The organic strips (the ends of which curl away from the surface in dried shells) become gradually covered by the foliose shell layer, beginning first between the strips and around the margin of each patch, enhancing the fingerprint effect.

I have not seen the flesh of this species, but TORIGOE (1981) reports that the right promyal passage is closed, the outer labial palp is extensively fused medially, and the anal appendage is digitiform.

The single living species, *Alectryonella plicatula* (Gmelin, 1791), may be rare and local, probably living in shallow subtidal depths, judging from the few lots in collections. It is known from the Indo-West Pacific faunal realm, from Madagascar to the Philippines, Ryukyu Islands, and western Caroline Islands. The organic strips regularly deposited along the protochomatal bands are unique to this species, and their alignment with the chomata furnishes the most convincing evidence that the chomata are derived from these bands.

Examination of the type specimens in the British Museum of Natural History showed that *Ostrea dubia* Sowerby, 1871, is a juvenile specimen, and *O. solida* Sowerby, 1871 (erroneously cited from the Gulf of Panama by him), is a completely white shell, externally, of *Alectryonella plicatula*.

Genus *Dendostrea* Swainson, 1835

Type, by subsequent designation of Herrmannsen, 1847: *Ostrea folium* Linné, 1758, Syst. Nat., Ed. 10, p. 699, No. 178. See Figures 17 and 18.

Lophini mostly of small to medium size (but to 85 mm high), irregularly subcircular to elongate dorsoventrally, with thin shells cemented by a variable part of the left valve, often with clasper spines which are usually short and adnate throughout their length. Both valves may be convex, the left more so than the right, and generally plicate, although the right valve may have plications limited to a small region; the plications are small, rounded, closely spaced, with rounded grooves between. The shell margin is generally zigzag along some part, even when plications of the right valve are poorly developed. The

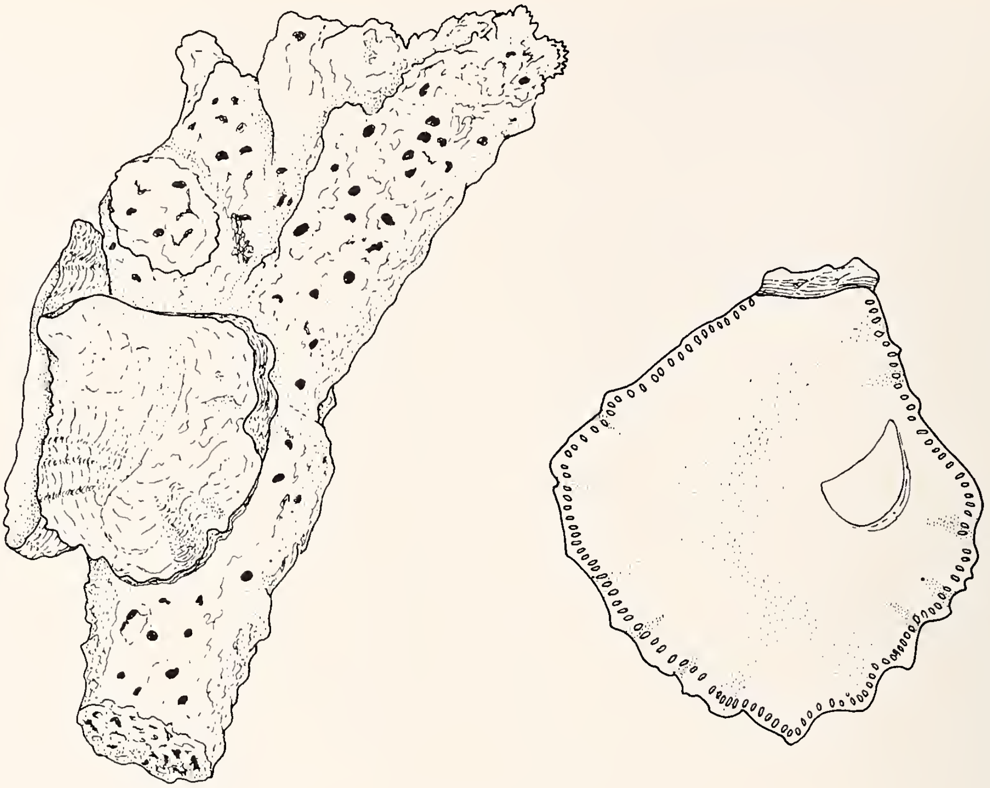

Figure 17

Dendostrea folium. Specimen on coral (*Acropora* sp.) at left, and the interior of the right valve, 23 mm high, of the front shell on the coral. From Abu Dhabi, Persian Gulf, 1 m deep, collected and loaned by John W. Tunnell, Jr.

external surfaces are without pustules, and usually smooth, often with a waxen texture, rarely with short lamellae at growth rests, which may form a few hyote spines on both valves. The exterior is often white, but usually blue or purple, sometimes rayed with darker stripes.

The shell interior is often white, varying to light or dark green; the chomata are usually only ostreine, limited to the margin near the hinge, but occasionally supplemented by lophine chomata in the right valve also, extending to the ventral margin.

The mantle lobes are thin, and often papillate internally; the outer labial palp is extensively fused in the midline, to three-fourths of its length. An accessory heart is developed behind the diaphragm, and it lacks tributaries. The anus has a large, fingerlike appendage (Figure 6), generally with sides inrolled and a cupped tip in the type species, *Dendostrea folium* (Linné, 1758), but it is flat and pointed in the other two known species.

Two of the three living species (there are no data for *D. mexicana*) are larviparous. *Dendrostrea folium* is extensively distributed in the Indo-West Pacific faunal realm; *D. frons* (Linné, 1758) occurs in the western, and probably also in the eastern Atlantic realms. *Dendostrea mexicanum* (Sowerby, 1871) occurs in the eastern Pacific (coast of Baja California), where specimens were rediscovered by Thomas Pulley and Constance Boone. The species live at shallow subtidal depths in protected waters of normal salinity in tropical and warm temperate seas. They are often associated with gorgonians, usually forming a leaflike, clasping ecomorph thereon, and on stony coral.

Tribe **Myrakeenini** Harry, new tribe

Lophinae in which only ostreine chomata are present; clasper spines are unknown in the living species. The outer surfaces of the shells are almost or entirely white, never extensively colored as in **Lophini**. A circular flange around the anus, drawn out to a fingerlike appendage on the outer margin, is present in ***Myrakeena*** *angelica,* the only species of the tribe of which the flesh has been available for study.

Genus ***Myrakeena*** Harry, gen. nov.

Type: *Ostrea angelica* Rochebrune, 1895, Mus. d'Hist. Nat. Paris, Bull., 1:241–242. Not figured. Holotype figured by KEEN (1971:81, fig. 167 [lower of the two]); see also Figure 19.

Myrakeenini in which the shells are mostly of moderate size (but to 100 mm high), subcircular, attached by cementation for half or less of the left valve's area. Both

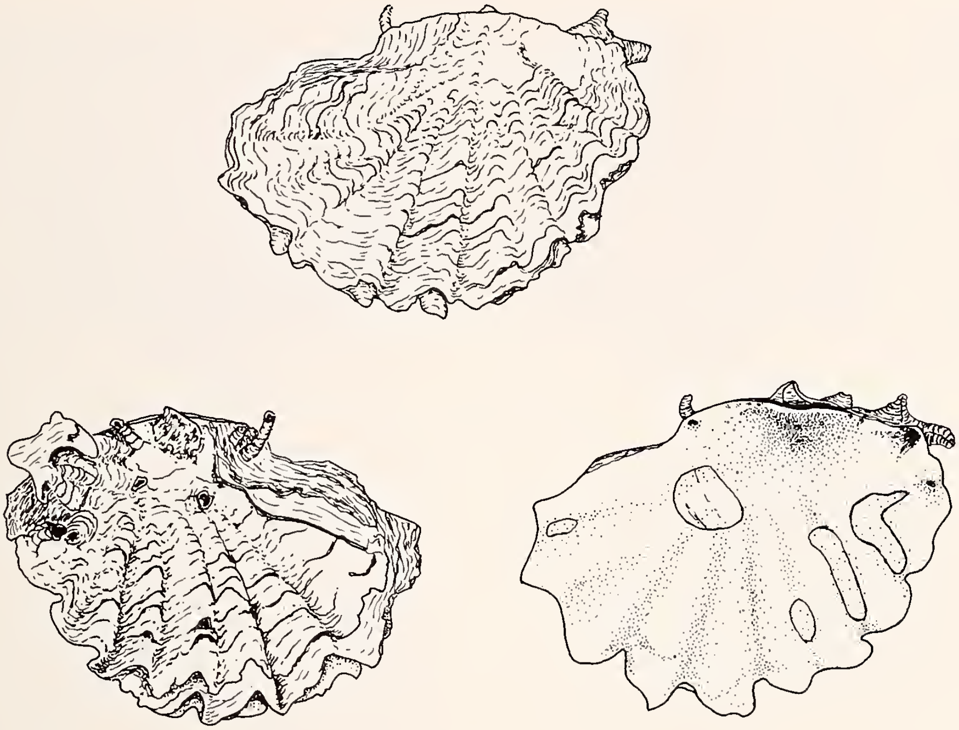

Figure 18

Dendostrea folium. Exterior of right valve above. Exterior of left valve at lower left, and interior of same at lower right. Shell is 43 mm high. Note patches of foliar layer of shell, forming chambers in the troughs near the periphery of the left valve interior. Only a few ostreine chomata are present, near the hinge. Three clasper spines of the left valve have holes opening to the interior, near the hinge. From Weld Island, Western Australia, shallow subtidal, collected and loaned by Constance E. Boone.

valves are slightly inflated, regularly plicate beyond attachment area by low, rounded ribs, ending in a zigzag marginal commissure. No hyote or clasper spines seem to form. The exterior is grayish white, occasionally with a linear stripe of dark purple in a few of the troughs between the ribs. The beaks are small, but the ligament is usually relatively long. The interior of the shell is white or light green. Lophine chomata are never formed, but ostreine ones always are, though small and occasionally only a few, near the ligament, or extending down the upper fourth of the valve margin.

The flesh is grayish, with thickened, opaque mantle lobes; the first neobranch unit behind the diaphragm is enlarged, and reaches to the heart; it does not receive tributaries. The outer labial palp is fused medially for about half of its length; the anus is surrounded by a circular flange which at the outer margin extends as a fingerlike appendage, tapering to an acute point, with sides curved so that it is semicylindrical. The reproductive habits are unknown.

The genus is named for A. Myra Keen, noted malacologist. ***Myrakeena** angelica* (Rochebrune, 1895), the only known species, seems to be limited to the Gulf of California, contrary to some statements in the literature. It lives in water of normal oceanic salinity, in protected situations at very low tide level and slightly deeper.

Genus *Anomiostrea* Habe & Kosuge, 1966

Type, by original designation: *Ostrea pyxidata* Adams & Reeve, 1850, Voy. Samarang, Moll., p. 72, pl. 21, fig. 19. Not *Ostrea pyxidata* Born, 1778, Index Mus. Caes. Vindobon., p. 93 (Pectinidae); renamed *Anomiostrea coralliophila* Habe, 1975.

Myrakeenini that are small, with the left valve hemispherical, the right one flat; the prismatic layer is light tan, but the interior of the shell is pure white. There are no clasper spines or chalk deposits. Numerous very small radial ribs, well defined, are on the peripheral part of the right and left valves. The ventral margin of the muscle scars is elevated. STENZEL (1971:N167) reproduced the original illustration of this species and that of SOWERBY (1871:pl. 9, figs. 16a, 16b) of the same specimen, but he thought it of uncertain affinity and possibly not an oyster. The following description of *Anomiostrea coralliophila* Habe, 1975, is based on this specimen, the holotype, which I studied at the British Museum of Natural History.

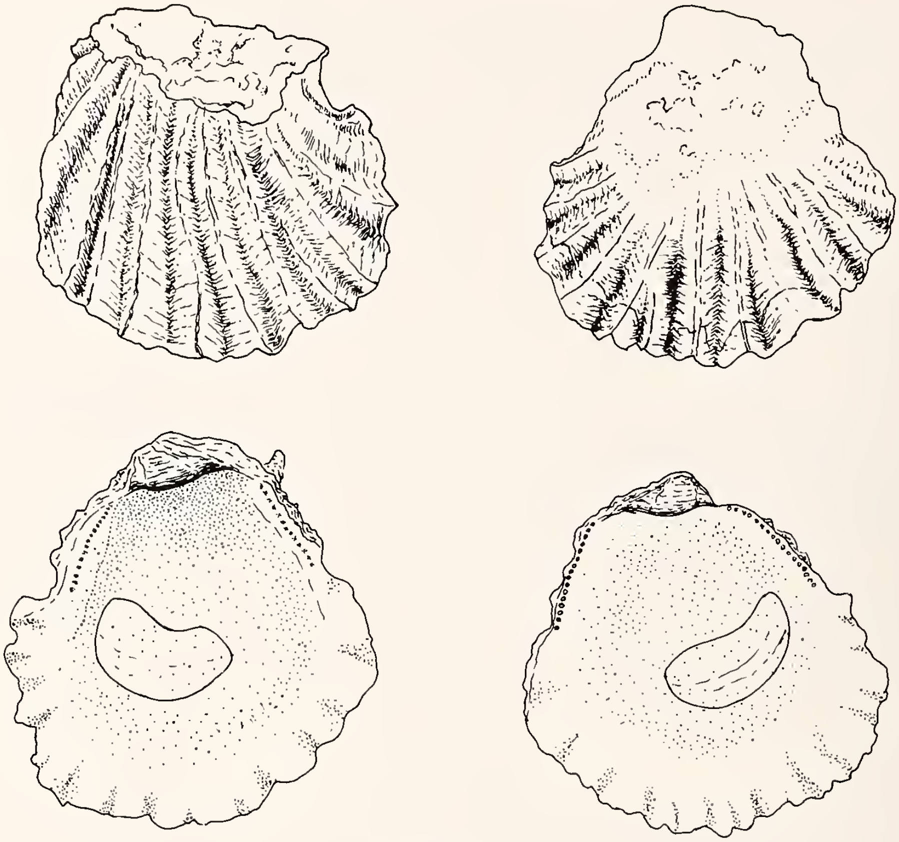

Figure 19

***Myrakeena** angelica.* A shell 77 mm high, from Bahía de Los Angeles, Baja California Norte, Mexico. Collected and loaned by Constance E. Boone.

The shell is small, 25 mm high, 25 mm long, 12 mm wide, and both valves are thin; it is subcircular in profile; the left valve is evenly swollen, nearly hemispherical, and the right valve is flat. The specimen is very light tan outside, and pure white within. The left valve was cemented to a flat, roughened surface by the umbonal fourth of its area, the attachment area being nearly at a right angle to the median plane of the shell. Thirty-six small, well defined, subacute radial ribs begin at the attachment area, and are separated by spaces about as wide as their diameters; some branch once, and a few short, intercalated ribs occur, so that the diameters of the rib-ends, around the shell margin, are those of their origin. Numerous growth rests give the ribs a subnodular appearance.

The initial third of the right valve's exterior is roughened, subnodular, with a waxen texture, being the xenomorphic representation of the coral to which the shell was evidently attached. Beyond that area the valve has ribs of the same size as those of the left valve. The marginal commissure is straight, not zigzag (but see below). The hinge is long (10 mm), the beaks low, orthogyrous, the ligamental scar divided into three equal parts. About 10 small pustules are in a line on the hind margin of the right valve, near the hinge, extending downward as far as the muscle scar and representing ostreine chomata. None were found on the anterior margin, and no pits were found on the margins of the left valve (possibly worn off through much handling of this delicate specimen). There is a moderate subumbonal cavity in the left valve and a smaller one in the right.

The adductor muscle scars are white and large; they appear to be subcircular with a flattened dorsal margin, but the latter is indistinct. The ventral margin of the scars in both valves are prominently elevated above the level of the shell surface, and the space ventral to the scar is partially covered by chambering.

The holotype was collected in the Philippines, and the specimens described by Habe & Kosuge (1966) were from Zamboanga, Mindoro, Philippines. They noted an "ovate" muscle scar which was "elevated," and a "crenulated" (zigzag) shell margin. The two lots at the U.S. National Museum of Natural History are from North Borneo (USNM 632887) and Jolo Id., Philippines (USNM 255013); they contain only five slightly worn left valves, evidently collected on the beach. Some show a crenulated shell margin, and distinctly reniform muscle scar, with lower margin elevated. The inner surface of some are corrugated by the ribs, and in others the corrugations are partially smoothed by chambering. RANSON (1967:272–273) listed the type specimen of this species in the British Museum and, based on specimens which he considered to be conspecific in other museums, he cited the species from Borneo, Ceylon, the Moluccas, and Java; he apparently overlooked the specimens in the U.S. National Museum, although he studied that very large collection.

The anatomy of the flesh is unknown.

Subfamily OSTREINAE Rafinesque, 1815

Ostreidae of small to medium or rarely large size; usually subcircular or subtriangular, rarely elongate dorsoventrally or falcate. Shell plications, when present, are limited to the left valve and frequently variable in development (but see ***Undulostrea***); the marginal commissure is rarely zigzag, and spines never develop on the shell exterior. The right valve tends to be flat; sculpture of the valves is varied, and distinctive for each genus. The beaks are small (exception: ***Pustulostrea***) and valves are not excessively thickened. The interior of the valves is usually white (less frequently in *Ostreola* and ***Pustulostrea***), often with chalky deposits or thin organic patches. The muscle scars are of the same color as the rest of the valve (exception: ***Pustulostrea***) and level with the shell surface. Ostreine chomata are generally present, except in ***Booneostrea***, and older specimens of *Ostrea* and ***Pustulostrea***.

The flesh is grayish, occasionally with black melanin pigment, usually limited to the margins of the mantle lobes, but bright orange or yellow pigments are absent. The right promyal passage is closed; the free surface of the mantle is rarely papillate in limited areas; the mantle lobes are thickened for glycogen storage in some species. A prominent accessory heart is present behind the diaphragm (except possibly in some **Cryptostreini**); it is a simple tube in most species, but receives as tributaries the adjacent neobranch units in *Ostrea*. The outer labial palp is slightly to extensively fused medially. The anal appendage, when present, is variable in form at the species level. Those species of which the reproductive habits are known are larviparous.

The species live subtidally to several meters depth, rarely extending to the lower intertidal zone in waters of constant, near normal salinity; most are tropical, but a few extend into warm temperate waters, and the species of one genus, *Ostrea*, are limited to cool temperate seas.

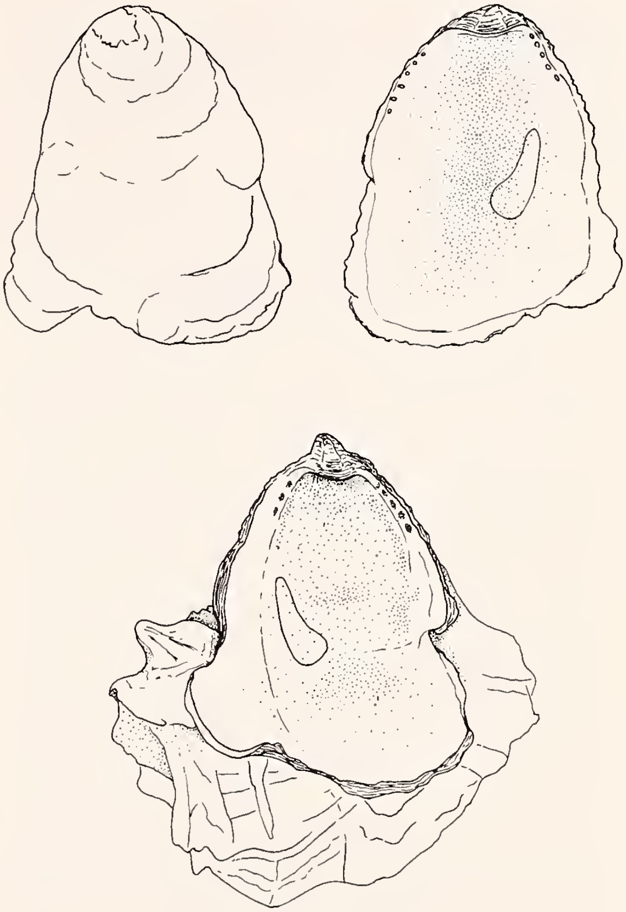

Figure 20

Ostreola stentina. Height, 35 mm. Left valve (below) is completely cemented to another shell. From Lake Tunis, Tunisia. Loaned by H. B. Stenzel.

The Ostreinae show a close relationship to the Lophinae in the completely closed right promyal passage and larviparous habit; these two phenomena are functionally associated in much of the literature, but without convincing justification. The bathymetric and salinity preference of the two subfamilies is about the same. The Ostreinae have regressed to various degrees in the amount of fusion of the outer labial palp medially, in the presence and shape of the anal appendage, and in the plication of the shell becoming much reduced; but they have retained the ability to produce chalk deposits, which the Lophinae have lost.

Three new characters have appeared in the Ostreinae which extend into the Crassostreinae: they have extended further into temperate areas than the Lophinae; the mantle has been thickened for storage of food (foreshadowed in ***Myrakeena*** in the Lophinae); and the right valve in several genera has developed peculiar imbricating lamellae along closely spaced growth lines (*Ostrea*, ***Booneostrea***, ***Teskeyostrea***, ***Pustulostrea***).

Tribe **Ostreini** Rafinesque, 1815, new tribe

Nom. trans. Harry, herein, *ex* Ostreidae Rafinesque, 1815.

Ostreinae in which the shell is small to large, subcircular to subtriangular to slightly elongate dorsoventrally, in which the right valve is nonplicate and flat or only slightly convex, the left valve more inflated and with plicate sculpture usually well defined. The right valve is sometimes washed or more often radially striped with blue, red, or purple.

Genus *Ostreola* Monterosato, 1884

Type, by original designation: *Ostrea stentina* Payraudeau, 1826, Cat. Moll. Corse, p. 81, pl. 3, fig. 3. See Figure 20; also fig. J112, p. N1140 in STENZEL (1971), who erroneously considered this genus to be a junior synonym of *Ostrea*.

Ostreini in which the shells are of small to medium size, and irregularly subcircular to somewhat elongate dorsoventrally. The prismatic layer of the right valve is light tan, non-lamellose, frequently with a wash or radial markings of various shades and tints of red, blue, and purple. The unattached part of the left valve is generally plicate. The interior of the shell is usually white, or green. Chomata are present throughout life, extending well down the anterior and posterior margins, and occasionally across the ventral part also.

The outer labial palp is fused medially for a fourth to a half of its length; the anus has a fingerlike appendage extending from the outer curve of its lip. The accessory heart does not receive adjacent neobranch units as tributaries.

Chiefly in shallow subtidal waters to a few meters depth, in tropical and temperate seas. Three species are known: *Ostreola stentina* (Payraudeau, 1826) in the eastern Atlantic, from the Mediterranean southward, possibly to South Africa; *Ostreola equestris* (Say, 1834) in the western Atlantic, from North Carolina to Argentina (*Ostrea spreta* Orbigny, 1841, is a junior synonym), and *Ostreola conchaphila* (Carpenter, 1857) in the eastern Pacific, from Alaska to Panama (*Ostrea lurida* Carpenter, 1864, is a junior synonym). The genus as restricted here is not known from the Indo-West Pacific faunal realm.

Genus *Ostrea* Linné, 1758

Type, by subsequent designation of Children, 1823: *Ostrea edulis* Linné, 1758, Syst. Nat., Ed. 10, p. 699. See fig. J190, p. N1137 in STENZEL (1971).

Ostreini with shells of moderate to large size, subcircular or subtriangular or rarely elongate dorsoventrally, the right valve nearly flat, with wide, overlapping, appressed, very thin and brittle lamellae, arising from rather closely spaced, evenly formed growth lines. The left valve is moderately inflated, with variable but usually distinct, small radial plicae, and a few growth rests which have only narrow, thick lamellae, or none at all. Chalk deposits in the inner shell layer are regularly present, in a distinctive pattern in older shells: a broad area behind and below the adductor muscle scar, with narrower extensions dorsad along both margins. The interior is usually white, occasionally washed with lavender or purple; similar color on the exterior of the shell is chiefly limited to young stages of growth. The chomata are very small, inconspicuous, ostreine, limited to the margin near the hinge, and sometimes disappearing in older specimens. No commissural shelf is defined in the shell.

The outer labial palp is fused medially for only a fourth of its length; the anus has a distinct circumferential flange, typically tapering to an obtuse point along the outer margin, so that it is heart shaped. The mantle lobes are thick. The accessory heart receives several adjacent neobranch units as tributaries.

The species live in cool temperate, euryhaline waters, usually at several meters depth, but an occasional specimen may be found at low tide level. Two subgenera are recognized.

Subgenus *Ostrea s.s.*

Shells generally grow to a larger size than those of the subgenus *Eostrea*; at the time of release the veligers have inflated umbos, extending well above the hinge line. The larval swimming period is about one to two weeks. Species of this subgenus are restricted to the northern hemisphere.

Two species are recognized: *Ostrea* (*Ostrea*) *edulis* Linné, 1758, in the eastern Atlantic, from Norway to Morocco and in the Mediterranean (with many junior synonyms); and *Ostrea* (*Ostrea*) *denselamellosa* Lischke, 1869, along the main islands of Japan and the adjacent shore of Asia.

Subgenus *Eostrea* Ihering, 1907

Type, by subsequent designation of Iredale, 1939: *Ostrea puelchana* Orbigny, 1841. Junior synonyms include *Anodontostrea* Sutter, 1917 (type: *Ostrea angasi* Sowerby, 1871, by subsequent designation of Finlay, 1928) and *Tiostrea* Chanley & Dinamani, 1980 (type, by original designation: *Ostrea lutaria* Hutton, 1873). See fig. J113, 1 and 2, p. N1141 in STENZEL (1971), which represents this species.

The umbos of the veligers are very flattened, not extending above the hinge line at time of release from the adult (see RANSON, 1967; CHANLEY & DINAMANI, 1980); the larval swimming period is about four days. A single species is recognized, *Ostrea* (*Eostrea*) *puelchana* Orbigny, 1841, which is circumglobal between 35° and 50°S latitude, including both coasts of South America, also southern New Zealand, southern Australia, and South Africa. Among the many junior synonyms are *Ostrea chilensis* Philippi, 1845, *Ostrea angasi* Sowerby, 1871, *Ostrea algoensis* Sowerby, 1871, and *Ostrea lutaria* Hutton, 1873.

Genus ***Nanostrea*** Harry, gen. nov.

Type: *Ostrea deformis* Lamarck, 1819, Anim. s. Vert., Vol. 6, pt. 1, p. 209. Not figured. Not *Ostrea deformis* Lamarck, 1806, Ann. Mus. Nat. d'Hist. Natur., Vol. 8, p. 164, Velin No. 57, fig. 4 (Palmer reprint, 1978) which is fossil, near Paris. *Ostrea deformis* Lamarck, 1819, is here renamed ***Nanostrea exigua***. See Figure 21.

Ostreini in which the shells are very small (to 12–15 mm high). The outer surface of the right valve is not lamellose, and the original light tan surface is frequently eroded to reveal shells entirely white, inside and out, or rarely radially streaked externally with lavender; they are usually cemented by most of the left valve, which has the upturned part plicate. The chomata are prominent, persistent, extending often completely around the margin. The outer labial palp is fused medially for three-fourths of its length; no anal appendage was present in the single preserved specimen of which the flesh was examined (USNM 769911, from Lizard Island, Queensland, Australia, at 10–11 m depth), but a pre-anal constriction gave the anus a knobbed appearance. The accessory heart is a simple tube, without tributaries.

Nanostrea exigua generally attaches to empty shells of other mollusks, in shallow lagoonal waters of coral reefs or on mudflats, in the tropical Indo-West Pacific faunal realm from the Red Sea to Hawaii. The original description of *Ostrea deformis* Lamarck, 1819, said the species is 8–11 mm long; the type locality was cited as "seas of Europe, etc, on other abandoned shells, most often in the interior of pinnas." RANSON (1967) examined the types in the Paris Museum and recognized this species as one from the Indo-West Pacific faunal realm.

Genus *Planostrea* Harry, gen. nov.

Type: *Ostrea pestigris* Hanley, 1846, Proc. Zool. Soc. London (for 1845), pp. 106–107. Not figured. See Figure 22.

Ostreini with shells of moderate size (to 75 mm high), very compressed, generally in one plane. The valves are not lamellose, the outer shell layer being continuous, with few growth rests, and little shell erosion. Small, semicylindrical plicae, widely spaced, are variously developed on the left valve only, and the surface is flat between these ribs. The chomata are exceptionally well developed, small, uniform, closely spaced near the hinge, along front and hind margins, which diverge in straight lines from the small umbos, forming an acute angle. In the left valve there is a wide marginal commissural shelf which is flat, well defined along its inner edge, and regularly thickened with chalk deposit. The outer surface of both valves is usually light to dark lavender, and often with numerous narrow, closely spaced, darker radial stripes of the same color.

A specimen with flesh from Hong Kong, dissected at the British Museum, had been dredged from 10 m depth. Additional specimens dissected were collected at low tide by Constance E. Boone, at Rowe's Bay, Townsville, Queensland, Australia. The mantle lobes are thin, transparent. Both left and right promyal passages are closed, but there is an incipient pocket on each side, narrow and deep, lateral to the pericardium, opening posteriad; the outer labial palp is fused medially for a fourth of its length. The anus seems to be surrounded by a narrow, circular flange of uniform width. The accessory heart is a simple tube, which does not receive adjacent neobranch units as tributaries.

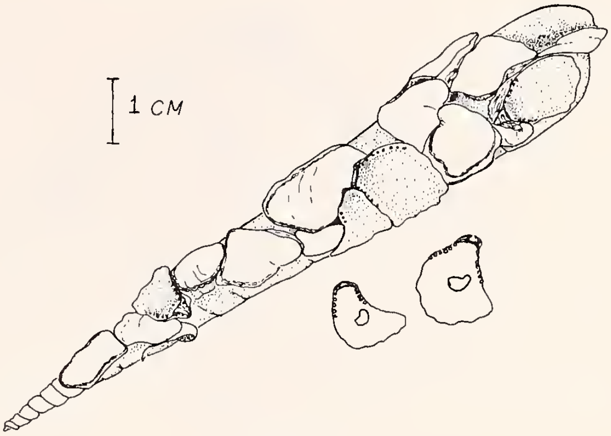

Figure 21

Nanostrea exigua. Several specimens on large, worn shell of *Terebra* sp. Tawi Tawi Ids., Philippine Ids. USNM 242291.

The single species, ***Planostrea*** *pestigris* (Hanley, 1846), is known only from a limited area in the Indo-West Pacific, being abundantly represented at the U.S. National Museum from the Philippines (type locality), but extending to Formosa, Thailand and North Borneo. An occasional specimen may occur at low tide, but most seem to have been dredged from a few to 100 m depth. Most are attached to shells of other mollusks, often to *Placuna placenta* (Linné, 1758).

Junior synonyms include *Ostrea rivularis* Gould, 1861, *Ostrea paulucciae* Crosse, 1869, and *Ostrea palmipes* Sowerby, 1871.

Tribe **Cryptostreini** Harry, new tribe

Ostreinae of small size, with delicate shells lacking radial plications on both valves. The coloring is uniformly light tan, with no purple washes or stripes. The chomata are reduced ostreine, or absent (***Booneostrea***). Irregular chalk deposits are infrequently present. The species live secluded in protected situations, usually in reduced light, in tropical and subtropical waters of normal oceanic salinity, subtidally to a few meters depth. Although neobranch units are present in the excurrent mantle chamber, an accessory heart was detected, with some doubt, only in ***Booneostrea***.

The species of the three monotypic genera each have distinctive form and sculpture, and they may not be a monophyletic group; the characters of the shell and flesh

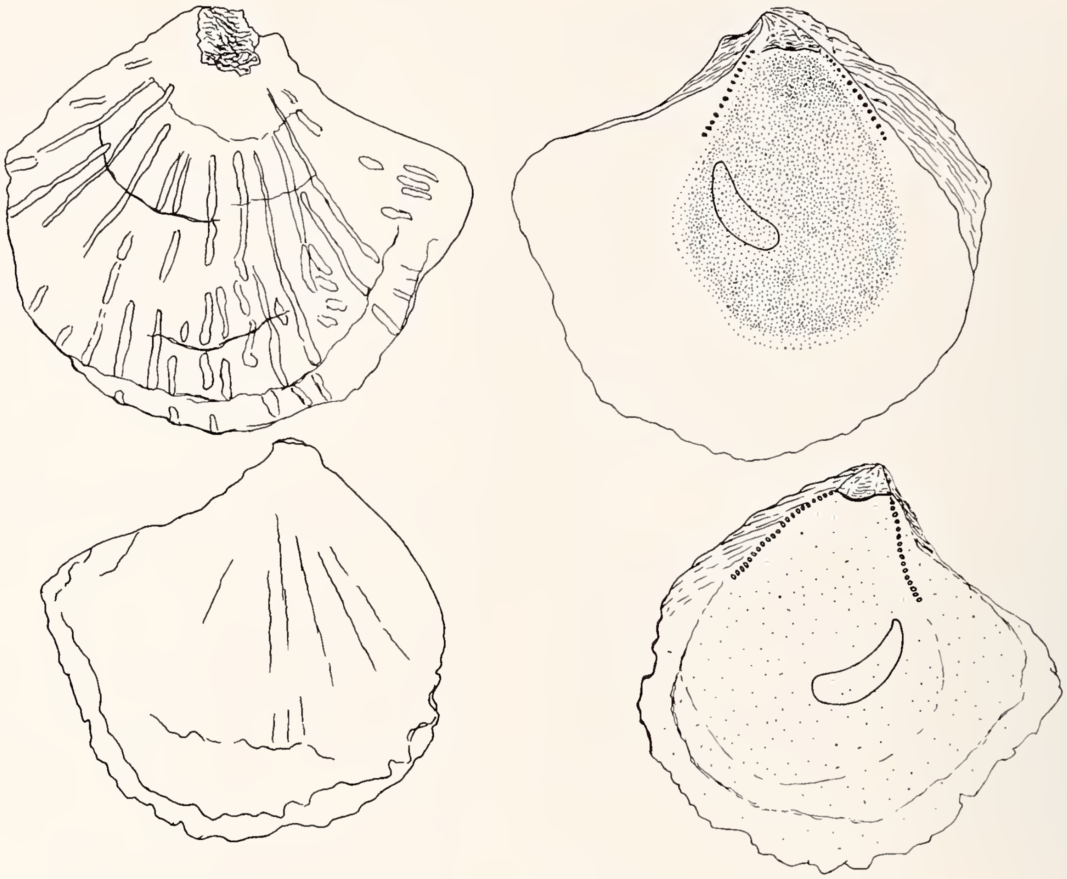

Figure 22

Planostrea pestigris. Height, 75 mm. Upper left: exterior of left valve, to show the small radial ridges. Lower left: exterior of right valve. Interiors of same valves are on right. Specimen collected by trawl, at 10 m depth, off Tambizan, North Borneo. USNM 666809.

suggest diminution or loss, which may result from their reclusive life habits. Larviparous specimens were found in all three species.

Genus ***Cryptostrea*** Harry, gen. nov.

Type: *Ostrea permollis* Sowerby, 1871, *in* Reeve's Conch. Icon., *Ostraea,* pl. 10, fig. 18a (18b is here excluded). See Figure 23.

Cryptostreini which are imbedded in sponge in postlarval life, rather than being cemented to firm substrate. The shells are small (30 mm high), very thin, only slightly inflated, inequivalve, but either valve may be the more inflated. The profile is subtriangular, subcircular or slightly elongate dorsoventrally; the beaks are of equal size, or the right one is smaller, and they are usually strongly twisted posteriad, rarely orthogyrous; the ligament tends to be drawn out along the dorsal third or more of the posterior margin; the anterior shell margin forms a large, acute angle with the axis of the ligament, and the posterior margin forms a large obtuse angle, sometimes nearly a straight line.

The outer shell layer is continuous over the surface, not interrupted by growth rests, and neither lamellose nor plicate, but often irregularly roughened. The color is uniformly light tan to darker brown. Small ostreine chomata are present, extending farther down along the anterior than the posterior margin. The interior of the shell is white, often slightly thickened with chalk deposit; it is not nacreous.

The outer labial palp is fused medially for the basal fourth of its length; the anus is surrounded by a distinct circular flange, extending as a flattened, tapering finger on the outer part of the rim.

Cryptostrea *permollis* (Sowerby, 1871) lives imbedded in the "bread sponge," a species of *Stellata* identical with or similar to *S. grubii* (see FORBES, 1964:454); the bathymetric range is from the very low intertidal zone to 154 m depth, in water of near oceanic salinity. It occurs in the northeastern Gulf of Mexico and off the coast of North

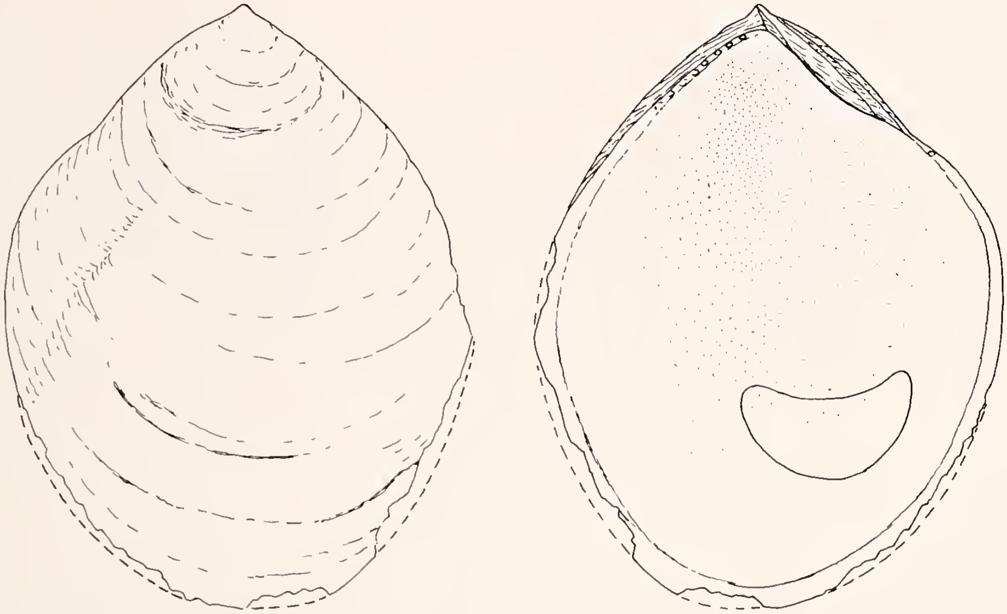

Figure 23

***Cryptostrea** permollis.* Right valve exterior and interior, of a shell 30 mm high, collected by Milton L. Forbes near Alligator Harbor, Florida, and loaned by H. B. Stenzel.

Carolina; literature records from the West Indies need verification.

STENZEL (1971) was unwilling to accept this species as a member of the Ostreacea, because of its peculiar habitat (personal communication), although it has been the most thoroughly studied of the non-commercial oysters, thanks to the papers by FORBES (1964, 1966). I have studied the anatomy of the flesh and shell from specimens collected by Forbes and given to Stenzel, as well as much other material collected by John W. Tunnell, Jr., from Florida, and several other sources.

***Cryptostrea** permollis* (Sowerby, 1871) was described from unknown locality; the specimens on whicn Sowerby's species was based were not found in the British Museum in October 1983, nor did RANSON (1967) seem to have found them.

Genus ***Teskeyostrea*** Harry, gen. nov.

Type: *Ostrea weberi* Olsson, 1951, Nautilus 65(1), pp. 6–7, pl. 1, figs. 1–4. See Figure 24.

Cryptostreini of small size (to 37 mm high), thin, subcircular, of uniform dark golden brown color. The left valve is extensively cemented to a rock, usually on the under side. The right valve is slightly convex, with appressed, lamellose extensions of the prismatic layer at numerous growth rests; the lamellae are thin, brittle, scarcely overlapping, and in larger specimens they show minute, radial ridges, evenly rounded, closely spaced, low, with linear grooves between; the interior is porcellaneous, often with one or two chalky pads. The chomata are ostreine, small, a few occurring on both anterior and posterior margins near the hinge.

The outer labial palp is fused for the basal fourth of its length; the anus is without any flange or appendage. The species is larviparous, and one specimen was gravid when collected in mid-December 1980.

The minute riblets of the lamellae of the right valve are similar to those of *Striostrea,* as noted by OLSSON (1951), who stated the type locality is Key West, Florida. The genus is named in honor of Margaret Teskey, for many years the Secretary of the American Malacological Union. She sent me live specimens with bits of the rock to which they were attached, from Big Pine Key, Florida, and empty valves collected at about 33 m depth off the Florida Keys by Pete Rosin. The U.S. National Museum has a single specimen (USNM 682581) taken by a diver in 2–4 m depth, off Cocoa Point, Barbuda, West Indies, and Constance E. Boone collected a specimen in the lagoon behind the island of Cancun, Yucatan, Mexico.

Genus ***Booneostrea*** Harry, gen. nov.

Type: *Ostrea cucullina* Deshayes, 1836, Cat. Moll. de l'Ile de la Reunion, pp. 36–37, pl. 32, figs. 7–8. See Figure 25.

Cryptostreini having small shells (to 28 mm high), which are thin, fragile, variously shaped but usually elon-

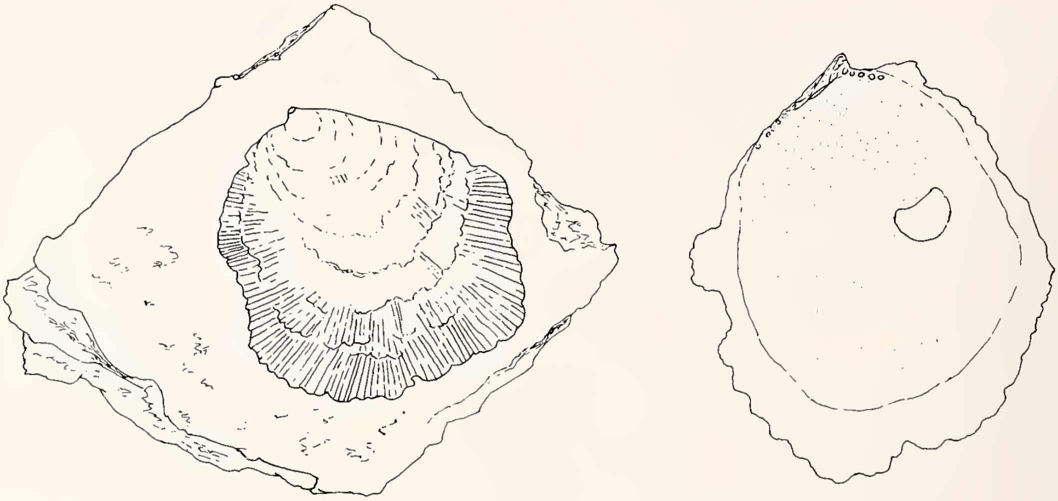

Figure 24

Teskeyostrea *weberi*. Exterior and interior of a right valve, 25 mm high; shell was attached to the underside of limestone rock, at low tide level, Big Pine Key, Florida. Collected and donated by Margaret Teskey.

gate oval dorsoventrally; the beaks are not prominent; the right valve is flat to slightly convex, and the left valve is very inflated. The right valve exterior is covered by a thin, light tan or white prismatic layer, which produces numerous, prominent, very fragile, imbricated lamellae beyond the first few millimeters of growth. These lamellae become more elevated ventrally, as the shell grows, and tend to be crossed by a few minute radial ridges, the radial sculpture becoming linear clefts in the edge of the lamellae near the ventral margin, giving the lamellae a scalloped appearance.

The left valve exterior is light tan or whitish, attached by cementation for about a third of its area in larger shells; there are no plications on the left valve, but prominent, broad lamellae may develop at growth rests, which are rather widely spaced; the lamellae are fragile, but thicker than those of the right valve, and they tend to project more from the shell surface; there is a slight tendency to develop the minute radial striae.

The internal surface is porcellaneous, whitish, and flushed with light tan. Chomata are completely absent, but the anterior and posterior ends of the bourrelet part of the ligament are extended as thin, tapering, organic lamellae, very delicate, for a short distance down both front and hind margins of the shell, in both valves.

The outer labial palp is fused medially for about a fourth of its length. The anus lacks a flange or appendage. The accessory heart was detected only in one of the several specimens examined; it is a simple tube without tributaries. Anatomical studies were made on four specimens found under an intertidal rock at Weld Island, about 30 km off Onslow, Western Australia, and three more from under a rock at Coconut Wells, 25 km north of Broome, Western Australia; one specimen of the latter lot, collected 10 September 1983, was larviparous. All of the above material was collected by Constance E. Boone, Secretary of the American Malacological Union, in whose honor the genus is named.

Booneostrea *cucullina* (Deshayes, 1836) is an oyster of the Indo-West Pacific faunal realm, known to extend from Reunion (type locality) to Australia and Japan. The U.S. National Museum has a few lots, from indefinite localities within this general area. It seems to live at low intertidal levels and to a few meters depth, in tropical waters of normal salinity. I found two left valves attached in a protected position to a mass of staghorn coral on the beach at Larentuka, Indonesia, evidently discarded by a fisherman. Junior synonyms include *Ostrea sedea* Iredale, 1939, from Australia, and *Ostrea sedea setoensis* Habe, 1957, from Japan. By the latter name the species was well illustrated by TORIGOE (1983).

Tribe **Undulostreini** Harry, new tribe

Ostreinae in which the shells are of moderate size (but to 90 mm high), thin, compressed, cemented by only a small area of the left valve, subcircular until about 20 mm high, then with disproportionate growth along the posteroventral margin of the shell, so that it becomes falcate, or L-shaped; several (two to four) large undulations develop along the anteroventral margin, with evenly rounded, broad troughs and crests, extending only a short way inward, and thus distinctly different from the usual plications of oysters. A single genus and species are recognized.

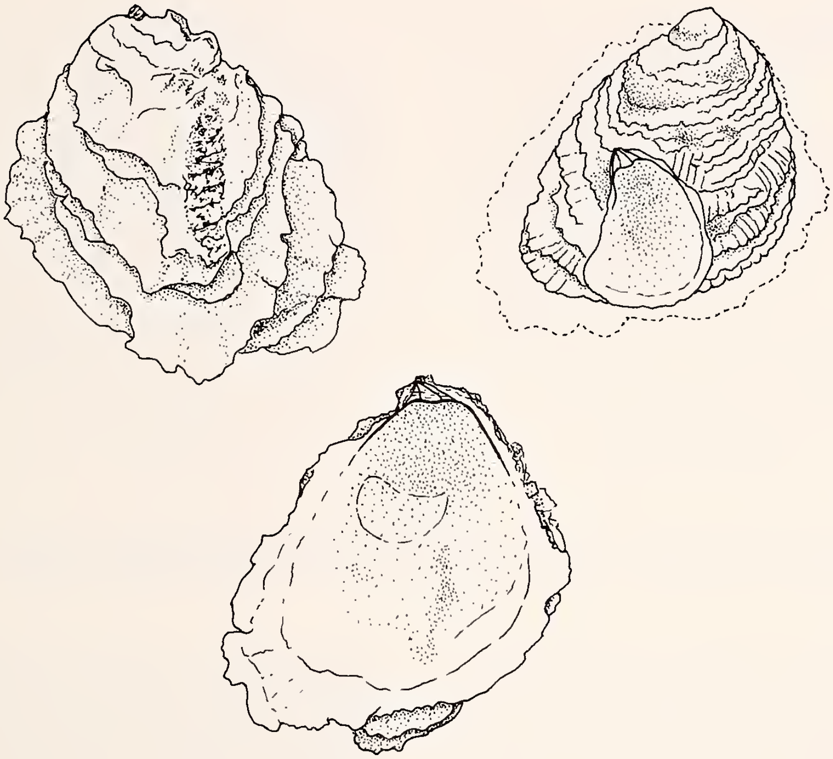

Figure 25

***Booneostrea** cucullina.* Exterior of left and right valves, and (below) interior of left valve. Height, 25 mm. Low intertidal zone, Weld Island, Western Australia. Collected and loaned by Constance E. Boone.

Genus *Undulostrea* Harry, gen. nov.

Type: *Ostrea megodon* Hanley, 1846, Proc. Zool. Soc. London (for 1845), p. 106. Not figured. See Figure 26.

The more conspicuous features of the unique species have been noted above; the outer shell layer of both valves is continuous, not lamellose at growth rests. The right valve is uniformly colored, purplish to light reddish brown, the left valve similarly colored or grayish, usually lighter than the right. The interior of both valves is grayish white. The chomata are ostreine, prominent, in a single line extending well down front and hind margins, but not to the ventral part. The beaks are small.

The outer labial palp is fused medially for about half its length. The accessory heart does not receive tributaries. There is no flange or appendage along the anal rim. Reproductive habits are unknown.

***Undulostrea** megodon* (Hanley, 1846) occurs infrequently from the Gulf of California and the lower west coast of Baja California to Peru (type locality), from low intertidal level to several meters depth, in water of normal salinity. It is generally attached to a shell fragment or even to the shell of a live mollusk, but possibly not to other oysters.

Tribe **Pustulostreini** Harry, new tribe

Ostreinae in which the beak of the left valve is enormously developed; both valves lack radial plicae, the left valve is not lamellose and usually it is extensively covered with pustules; the right valve exterior is densely covered with appressed lamellae. The single species closely resembles *Striostrea* in some shell characters, but it is distinctly ostreine in having a closed right promyal passage.

Genus *Pustulostrea* Harry, gen. nov.

Type: *Ostrea tuberculata* Lamarck, 1804, Ann. Mus. Nat. d'Hist. Natur. (Paris) 4:358, pl. 67, fig. 1. See Figures 27 and 28.

The shells are of medium to large size (to 90 mm high), compressed, elongate dorsoventrally, generally arched (concave to left) along the axis of height; the beak of the left valve is disproportionately large, often being half the height of the shell. The attachment area is small, and apparently absent on some shells. The left valve exterior is without plications, but usually has low, rounded pustules, closely but irregularly spaced, variably produced on the surface. The right valve is flat, subcircular, with its

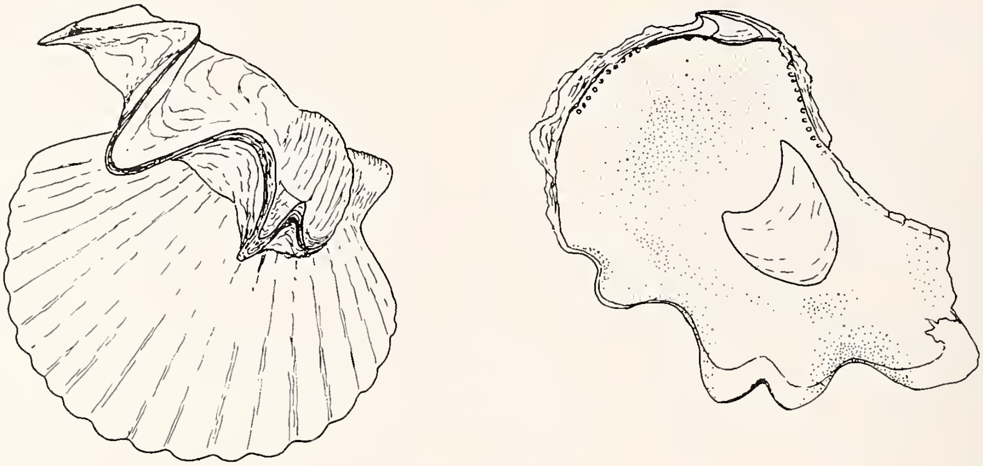

Figure 26

***Undulostrea** megodon*. Specimen 35 mm high, attached to *Argopecten circularis* (Sowerby, 1835), from low intertidal zone in Laguna San Ignacio, Baja California, Mexico. Collected and loaned by Thomas E. Pulley.

beak only slightly produced, and its outer shell layer covered with closely spaced, smooth, fragile, appressed lamellae at the growth rests. The outer surface of the left valve is pale gray, that of the right valve light brown.

The hinge is exceptionally long, and the left umbonal cavity is often deep; the muscle scar of the left valve is usually dark brown (the color not limited to the scar, but extending beyond), that of the right valve is white. The interiors of both valves tend to be subnacreous and washed with brown or blue. The chomata are ostreine, large, elongate normal to the valve margin, widely spaced, extending downward two-thirds of the height on both margins, and occasionally absent in older shells.

The outer labial palp is extensively fused medially for

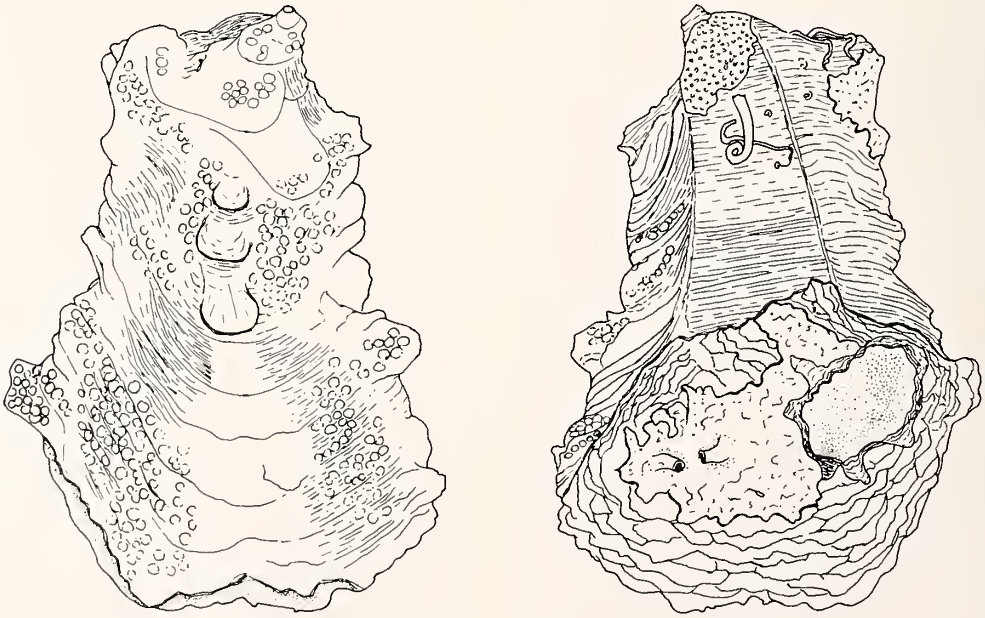

Figure 27

***Pustulostrea** tuberculata.* Exterior of valves of a shell 70 mm high. New Hebrides Ids. USNM 787959. See Figure 28.

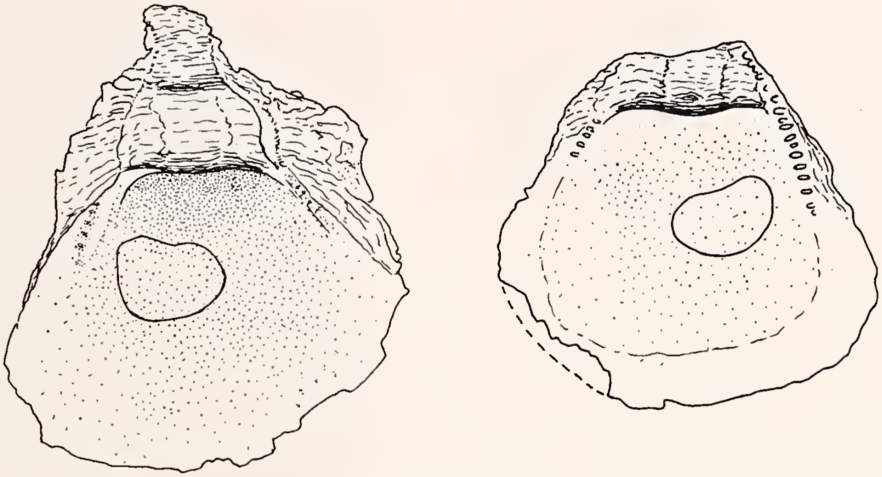

Figure 28

***Pustulostrea** tuberculata.* Height, 90 mm. Interior of the valves of a second specimen from lot USNM 787959, from the New Hebrides Ids. See Figure 27.

two-thirds of its length. The anus is surrounded by a distinct flange, drawn out to a tapering, fingerlike appendage on the outer rim. The mantle lobes are thick. Flesh of several specimens of the U.S. National Museum were examined; these were collected by Thomas Waller in the New Hebrides Islands, after RANSON (1967) had completed his study of oysters at that museum.

This species is evidently rare and local; according to the records published by RANSON (1967), it occurs from the islands off the west coast of the Malay Peninsula to Singapore, throughout Indonesia and eastward to the New Hebrides, evidently in shallow water of high salinity, and probably usually associated with coral reefs. Reproductive habits are unknown. Junior synonyms include *Ostrea rufa* Lamarck, 1819, and *Ostrea australis* Lamarck, 1819.

Subfamily CRASSOSTREINAE Torigoe, 1981

Ostreidae with shells of medium to large size, usually elongate dorsoventrally, occasionally subcircular. The left valve is usually deeply concave, and the right one is usually nearly flat. Shell plications are usually limited to the left valve, often indifferently developed or absent. The early part of the right valve exterior has continuous growth of the outer shell layer, and later it often forms fragile, appressed, overlapping lamellae, but the outer surface is frequently eroded during life, obliterating the sculpture. The chomata are ostreine, or absent. The muscle scars tend to be more darkly colored than the surrounding shell, in one or both valves.

The mantle lobes are thickened and used for storage of glycogen. The right promyal passage is open over the pericardium and lower half of the visceral mass, and thus is about half as extensive as that of the Pycnodonteinae. The outer labial palp is only slightly fused medially, one-fourth its length or less, and in some species it is unfused. The anus is usually without an appendage, but in some species it has a circular flange. The accessory heart is well developed, various in form, but it does not receive adjacent neobranch units as tributaries. The species that have been studied do not brood their larvae.

Species are chiefly tropical and subtropical, but some species of *Crassostrea* extend also into cool temperate water. These oysters tend to live intertidally or at shallow subtidal depths.

The Crassostreinae have retained the ability to secrete non-vesicular chalk deposits. They have continued the reduction of the fusion of the labial palp and formation of an anal appendage. Whether the partly open (or partly closed) right promyal passage is a regressive or progressive character is a moot question. The species of this subfamily have moved into shallower depths, thus experiencing greater fluctuation of environmental factors, than all other oysters. They tend to be large, with thick, food storing mantle lobes in all species, and they are generally abundant where they occur, being, by these characters, preeminent as the oysters of commerce.

Tribe **Striostreini** Harry, new tribe

Crassostreinae in which ostreine chomata are usually prominent (lost in some larger shells of *Striostrea,* and lacking in some ecomorphs of *Saccostrea*), often extending to the ventral margin. Thick, broad conchiolin deposits are frequent, chiefly in the right valve. The left valve has a propensity, variable within a species, to become enormously thickened by chambering, so the thickness may equal or exceed the height of the valve. Chalk deposits are infrequent. The hinge line is usually long in proportion to other shell dimensions, and the left beak is often produced, with a large subumbonal cavity.

Limited to the tropics and subtropics, these oysters prefer normal salinity; although occasionally associated with red mangroves, most species live exposed to strong surf, attached to rock, but they avoid coral and limestone. The tribe is present in the eastern Atlantic, Indo-West Pacific and eastern Pacific faunal realms, but is apparently absent from the shores of the western Atlantic.

Genus *Saccostrea* Dolfuss & Dautzenberg, 1920

Type, by monotypy: *Ostrea saccellus* Dujardin, 1835, Mem. Geol. Soc. France 2(2):272 (Miocene fossil of France), which is a junior synonym (*fide* STENZEL, 1971) of *Ostrea cucullata* Born, 1778. See fig. J104, p. N1132 and fig. J105, p. N1133 in STENZEL (1971).

Striostreini in which the shell is of medium size, the attached part of the left valve of larger shells forming about half the total area of the valve or less, and the upturned part of the left valve with prominent, regular and continuous plications, often acutely crested, with broad, flat or concave troughs between. The right valve is flat, but projecting along the margin are short lobes, coordinate with the plications of the left valve; a few flattened plications, closely spaced, may develop on the right valve as the marginal lobes are extended.

Juvenile shells (to 30 mm high) may develop on the right or on both valves a few to many short, recurved, semicylindrical spines, usually colored dark purple; these may be abundant on one specimen and absent on an adjacent one of the same size; they are generally worn off in larger shells. In protected situations the right valve of larger shells may be densely covered with imbricated lamellae, brown or purple, which have no radial striations (contrast *Striostrea s.s.*), but most right valves, exposed to the action of the waves, are eroded in a characteristic fashion. The abrasion forms broad, irregularly rounded pits, showing sharp or beveled contours, with the bottom of the pits often floored by a sheet of dark borwn, thick conchiolin (which becomes very brittle and fractures in dry shells).

The hinge line is long, the left beak is often very large, and the left subumbonal cavity may often be as large as the rest of the shell's interior; ostreine chomata are present, small but prominent, often widely spaced and extending to and across the ventral margin. Inside, the valves are essentially white, but a wide blue or purple margin may be present; the interior is porcellaneous; large brown patches of thick conchiolin are frequent, chiefly in the right valve. The attachments of the secondary mantle margin retractor muscles often leave a line of small, circular scars parallel to the front and hind margins of the shell. The valves are not brittle and flaky as in *Striostrea s.s.* One or both adductor muscle scars may be darker than the general shell interior.

The outer labial palp is fused medially about a fourth of its length; there is no anal flange or appendage. In preserved specimens the accessory heart is an enormous, inflated, thin walled, flabby sac. The mantle margin is generally lightly washed with black pigment and there are a few granules of bright yellow pigment on the inner and middle mantle margin lamellae and their papillae; this yellow pigment is characteristic of the genus and often persists in specimens preserved in alcohol.

Limited to the tropics or slightly beyond, the species are sometimes attached to prop roots of red mangroves, but they live chiefly attached to non-calcareous rock in the intertidal zone, where they are subject to strong wave action. They probably do not live naturally subtidally.

Two species are known. *Saccostrea cucullata* (Born, 1778) occurs along the tropical coast of West Africa and offshore islands, around the Cape of Good Hope and into the Indo-West Pacific to southern Japan, southeast Australia, northern New Zealand, and possibly somewhat eastward, but it seems not to reach the extreme eastern part of the Indo-West Pacific faunal realm (Hawaii to Society Islands). The list of junior synonyms is long. A second species, *Saccostrea palmula* (Carpenter, 1857), occurs in the eastern Pacific, from San Ignacio Lagoon, west coast of Baja California, to Panama and the Galapagos Islands.

Genus *Striostrea* Vyalov, 1936

Type, by original designation: *Ostrea procellosa* "Valenciennes" Lamy, 1929, which is a junior synonym of *Ostrea margaritacea* Lamarck, 1819. See Figure 29. Also see fig. J107, p. N1135, and fig. J108, p. N1136, in STENZEL (1971).

Two subgenera are recognized.

Subgenus *Striostrea s.s.*

Striostreini in which the shell grows to large size (to 200 mm or more high), usually elongate dorsoventrally but sometimes subcircular, generally attached by nearly the entire area of the left valve, which, especially in elongate shells, may become enormously thickened, forming a broad pedicel, with no upturned (or idiomorphic) part, but merely a surface formed by earlier shell margins. Right valve not plicate, but covered with imbricated, brown, brittle lamellae, which usually have closely spaced, very small radial riblets or striae continuous across them. In larger shells, the lamellae are mostly worn off.

The hinge line is usually long, and the left beak enlarged; the valves are very brittle, breaking with a flaky, jagged margin and often separating smoothly between successive deposits of the foliar shell layer. The interior is distinctly subnacreous, iridescent, occasionally white but more often mottled and washed with dark brown, blue, or purple. The chomata are large, often elongate, widely spaced, usually extending far down both front and hind margins, but sometimes absent from larger shells. One or both muscle scars are often distinctively colored.

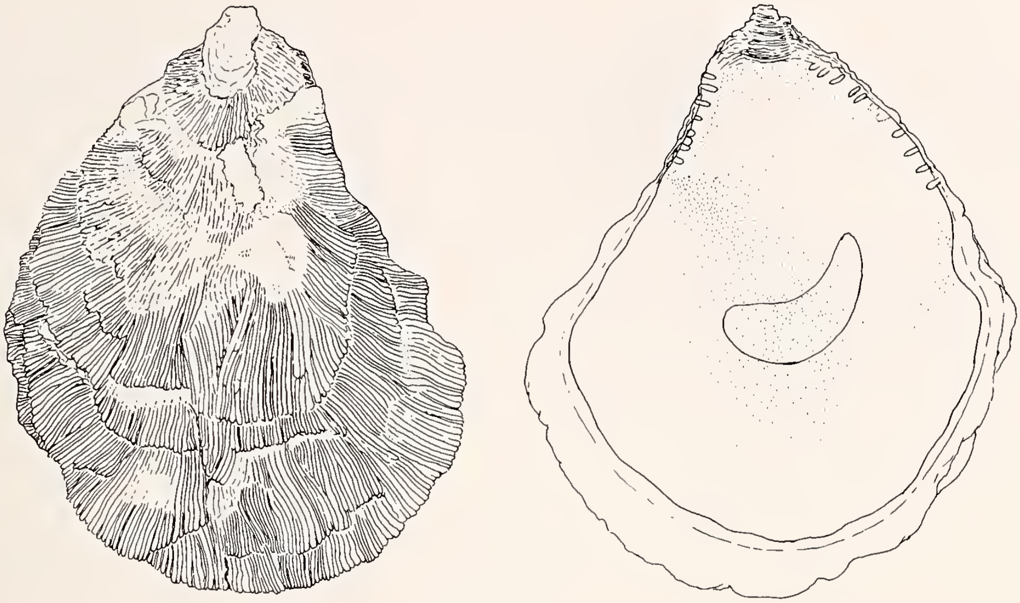

Figure 29

Striostrea prismatica. Exterior and interior of right valve, of a juvenile shell only 45 mm high. Collected at Puerto Vallarta, Jalisco, Mexico, by the author.

The outer labial palp is fused medially for a fourth of its length. The anus is simple, without flange or appendage. The accessory heart is large, but compact and cylindrical. There is no bright yellow pigment in the mantle margin; the mantle lobes are thick and muscular toward their margins. In the only species of which the flesh has been available for study, *Striostrea prismatica* from western Mexico, the gill suspensory septa are discontinuous.

Three species are known in the typical subgenus, each from a limited area: *Striostrea* (*Striostrea*) *margaritacea* (Lamarck, 1819) is found along the coast of tropical West Africa to South Africa (records of it from Madagascar may be based on the next subgenus?); *S.* (*Striostrea*) *circumpicta* (Pilsbry, 1904) occurs in southern Japan; and *S.* (*Striostrea*) *prismatica* (Gray, 1825) lives in the tropical eastern Pacific (Figure 29). The species live chiefly in the shallow subtidal zone, attached to non-calcareous rock in strong surf of normal salinity.

Subgenus *Striostrea* (***Parastriostrea***)
Harry, subgen. nov.

Type: *Ostrea mytiloides* Lamarck, 1819, Anim. s. Vert., Vol. 6, pt. 1, pp. 207–208. Not figured. See Figure 30.

Striostrea of large size (to 120 mm high), generally adhering to red mangrove roots, the left valve not excessively thickened, but attached by half the valve or less, the free part of the valve not plicate but occasionally vaguely undulate. Right valve covered with imbricated, dark purple lamellae which have no radial striations.

The hinge is long, but the left beak is rarely enlarged; the interior is porcellaneous. There are large ostreine chomata similar to those of *Striostrea s.s.,* which in larger shells usually extend completely around the ventral margin. The shell interior is white or washed or mottled with brown or various shades of purple, and the margin is usually dark purple.

The flesh is similar to that of the typical subgenus, but whether the suspensory septa of the gills are continuous has not been determined. This monotypic genus extends from Samoa to the Philippines, Indonesia (type locality), northwestern Australia, India, and Zanzibar. The species was figured by SOWERBY (1871:pl. 2, fig. 3).

Tribe **Crassostreini** Torigoe, new tribe

Nom. trans. Harry, herein, *ex* Crassostreinae Torigoe, 1981.

Crassostreinae in which the chomata are absent throughout life; the large shells tend to be elongate dorsoventrally, but are often subcircular. The adductor muscle scars of both valves tend to be colored dark purple, brown or blue, but in some populations, particularly in the tropics, one or both scars may be lightly colored or white. The interior of the valves is white, often washed with purple marginally, especially in tropical populations. Chalk deposits are frequent and extensive; conchiolin deposits occur, but chiefly as thin, small patches formed as preliminary reactions to shell invaders. Chambering is occasional, but the left valve never becomes as thick as it

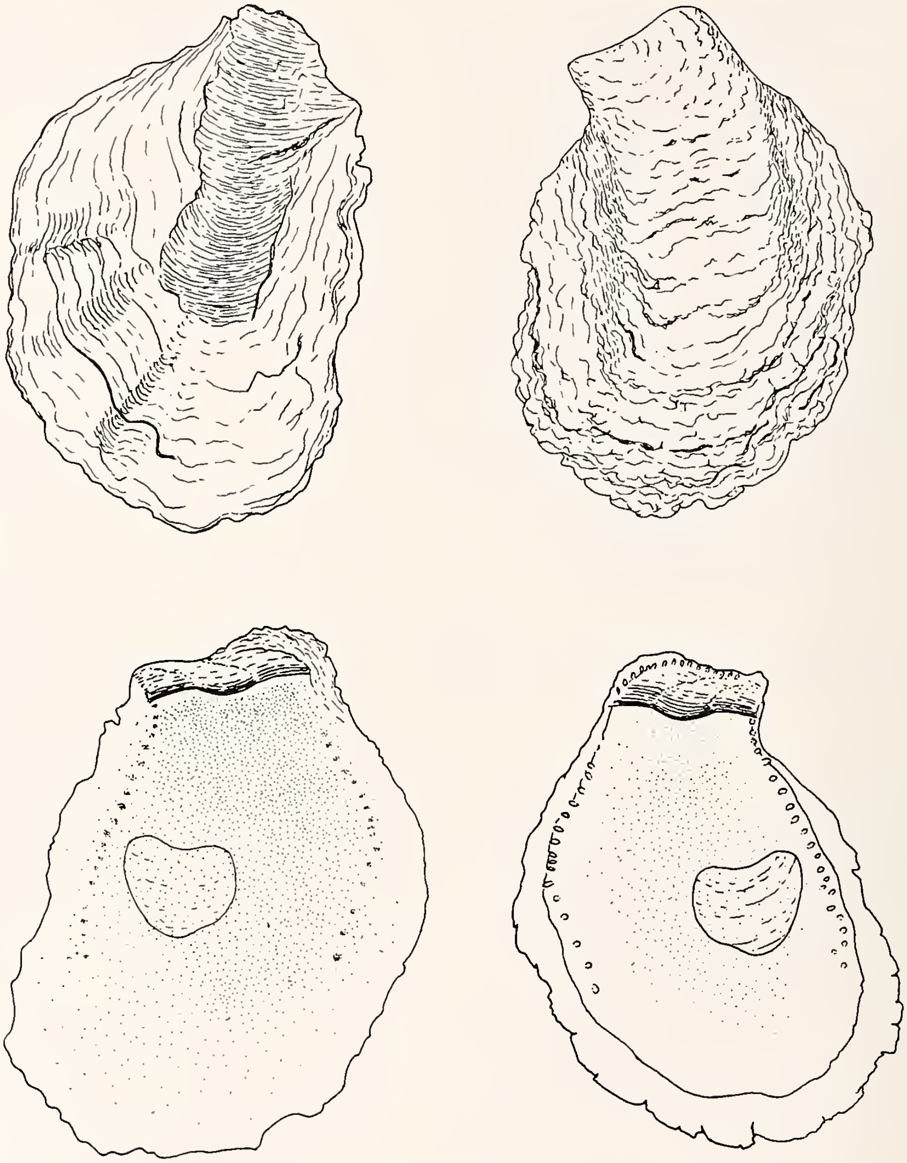

Figure 30

Striostrea (***Parastriostrea***) *mytiloides*. Height, 120 mm. Left valve (upper and lower left) cemented to prop root of a red mangrove. Right valve exterior (upper right) covered by closely appressed, deep bluish purple lamellae. From Efate Id., New Hebrides Ids., collected by Thomas Waller.

does in the Striostreini. The hinge line is usually short, and the left beak is rarely extended.

The species are chiefly limited to estuarine conditions, preferring brackish water of about 15–30 ppt salinity; in the tropics they are often associated with mangroves, sometimes where hypersaline conditions occur. Where they occur naturally, they seem limited to the shores of continents and larger islands nearby, and although present in all four major faunal realms, they seem nearly limited to the northern hemisphere; natural populations may extend only slightly below the equator (Brazil, possibly Indonesia also?).

Genus *Crassostrea* Sacco, 1897

Type, by original designation: *Ostrea virginica* Gmelin, 1791, Syst. Nat., Ed. 13, p. 3336. See the extensive illustrations in Galtsoff (1964) and fig. J101 (1a–h only), p. N1129, in Stenzel (1971).

The characters of the shell noted for the tribe are those of the single genus. The outer labial palp is not fused medially in *Crassostrea virginica,* but is slightly fused in *C. gigas.* The rectum ends at the posteroventral curve of the adductor muscle, being thus very short, and the anus is usually without any appendage (but a circular flange

Table 1

Comparison of the number of species, distribution and environment of the genera and subgenera of living oysters.

					Geographic location[1]				Climatic zones[2]			Depth[3]				Special habitat[4]			Salinity[5]	
Family	Subfamily	Tribe	Genus and subgenus	No. of species	East Atlantic	West Atlantic	East Pacific	Indo-West Pacific	Tropical	Warm temperate	Cool temperate	Most below 50 m	Subtidal to a few m	Low intertidal	Mid intertidal	Mangrove associate	Coral reef associate	Exposed to strong surf	Normal salinity	Brackish water
Gryphaeidae	Pycnodonteinae	**Hyotissini**	*Hyotissa*	1			X	X	X				X				X	?	X	
			***Parahyotissa* s.s.**	2	X	X			X	X			X				?		X	
			***P.* (*Pliohyotissa*)**	1			X		X	?			?	X					X	
			***P.* (*Numismoida*)**	1				X	X				X				X		X	
		Neopycnodontini	*Neopycnodonte*	1	X	X		X	X	X	?	X							X	
Ostreidae	Lophinae	**Lophini**	*Lopha*	1				X	X				X				X		X	
			Alectryonella	1				X	X				X				X		X	
			Dendostrea	3	X	X	X	X	X	X			X				X		X	
		Myrakeenini	***Myrakeena***	1			X			X			X	X					X	
			Anomiostrea	1				X	X				X				X		X	
	Ostreinae	**Ostreini**	*Ostreola*	3	X	X	X		X	X	X		X	X					X	
			Ostrea s.s.	2	X			X			X		X						X	
			O. (*Eostrea*)	1	X	X	X	X			X		X						X	
			Nanostrea	1				X	X				X				X		X	
			Planostrea	1				X	X				X			?			X	
		Cryptostreini	***Cryptostrea***	1		X			X				X						X	
			Teskeyostrea	1		X			X				X	?					X	
			Booneostrea	1				X	X				X	X					X	
		Undulostreini	***Undulostrea***	1			X		X	X			X	?					X	
		Pustulostreini	***Pustulostrea***	1				X	X				X	?			X		X	
	Crassostreinae	**Striostreini**	*Saccostrea*	2	X		X	X	X	X					X	X		X	X	?
			Striostrea s.s.	3	X		X	X	X	?			X	X		?		X	X	?
			***S.* (*Parastriostrea*)**	1				X	X	?				X		X		?	X	?
		Crassostreini	*Crassostrea*	4	X	X	X	X	X	X	X		X	X	?	X				X

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[1] Geographic location: includes all species of each genus and subgenus. Some species occur in two areas (*Hyotissa hyotis*, ***P.* (*Parahyotissa*)** *mcgintyi*, *Neopycnodonte cochlear*, *Dendostrea frons*, *Saccostrea cucullata*), but other species are limited to one of the four areas.

[2] Climatic zones: includes all species of a genus or subgenus.

[3] Depth, very generalized; the depth indicated is considered the "optimum," or where the species is most abundant, based on data presently available.

[4] Special habitat: the special habitat attributed to the taxa shown does not mean that the species are limited to that situation; no special habitat is known for species of some taxa.

[5] Salinity: very generalized.

is present in *C. gigas*); the accessory heart is a thick, muscular, cylindrical tube without tributaries.

Four species are recognized, each with a long list of junior synonyms. *Crassostrea angulata* (Lamarck, 1819) occurs in the eastern Atlantic, from the equator northward to the Mediterranean and Atlantic coast of the Iberian Peninsula; it has been introduced into southwestern France. *Crassostrea virginica* (Gmelin, 1791) is found in the western Atlantic, from Brazil northward through the Caribbean and Gulf of Mexico, including the Antilles, to the

Table 2

Comparison of shell traits of genera and subgenera of living oysters.

Family	Subfamily	Tribe	Genus or subgenus	Large size[1]	Medium size[1]	Small size[1]	L valve plicate[2]	R valve plicate[2]	Hyote spines[3]	Erect lamellae[4]	Appressed lamellae[4]	No lamellae[4]	Organic deposits[5]	No chalk deposits[6]	Vesicular chalk dep.[6]	Non-vesic. chalk dep.[6]	Commissural shelf[7]	Musc. scar circular[8]	Musc. scar reniform[8]	Vermicular chomata[9]	Lophine chomata[9]	Ostreine chomata[9]	Chomata absent always[9]	Chomata may disappear in larger shells[9]	Musc. scar distinctive in color[10]	Surface pustulose[11]
Gryphaeidae	Pycnodonteinae	**Hyotissini**	*Hyotissa*	X			F	F	F	F		R	R		X		X	X		X						R
			Parahyotissa *s.s.*		X		F	F	F	F		R	R		X		X	X		X						
			***P.* (*Pliohyotissa*)**		X		R	R				X	F		X		X	X		X						
			***P.* (*Numismoida*)**		R	X						X			X			X								
		Neopycnodontini	*Neopycnodonte*		X		R					X	?		X		X	X		X		X				
Ostreidae	Lophinae	**Lophini**	*Lopha*		X		X	X	X			X	X	X					X		X					X
			Alectryonella		X		X	X	R			X	X	X					X		X	X				X
			Dendostrea		X		X	X	F			X	?	X					X		X	X				
		Myrakeenini	***Myrakeena***		X		X	X				X	X	X					X			X				
			Anomiostrea			X	X	X				X		X					X			X				
	Ostreinae	**Ostreini**	*Ostreola*			X	X					X	X			X			X		X					
			Ostrea s.s.	X			X				X		?			X			X		X			X		
			O. (*Eostrea*)	X			X				X		?			X			X		X			X		
			Nanostrea			X	X					X	?			X			X			X				
			Planostrea		X		X					X	?			X	X		X			X				
		Cryptostreini	***Cryptostrea***			X						X	?			X			X			X				
			Teskeyostrea			X					X		?			X			X			X				
			Booneostrea			X					X		?			X			X				X			
		Undulostreini	***Undulostrea***[12]		X		X	X				X	?			X						X				
		Pustulostreini	***Pustulostrea***		X						X		X			R			X			X		X	X	X
	Crassostreinae	**Striostreini**	*Saccostrea*[13]		X		X	R	F		X		X			X			X			X			X	
			Striostrea s.s.	X							X		X			X			X			X		X	X	
			S. (***Parastriostrea***)	X							X		X			X			X			X				
		Crassostreini	*Crassostrea*	X			R	R			R		X			X			X				X		X	

F = frequently; R = rarely; X = generally as indicated.

[1] Size: indicates the size usually attained.

[2] Plications: these vary in shape, spacing and prominence in different species. The lamellar striations of *Striostrea* and ***Teskeyostrea*** are not considered to be plications.

[3] Hyote spines: these vary in form and occurrence in different species.

[4] Lamellae of the right valve only.

[5] Organic deposits: may be absent in some specimens of species in which they generally occur.

[6] Chalk deposits: variable within most species.

[7] Commissural shelf: considered to be present if the inner margin is usually sharply defined.

[8] Shape of the adductor muscle scar.

[9] Chomata: in *Neopycnodonte* the chomata are intermediate between the two types indicated; both lophine and ostreine chomata may be present in some Lophinae.

[10] Muscle scar distinctively colored from the rest of the shell's interior; the color may not be limited to the area within the scar's margin.

[11] Pustules of the outer surface of the shell vary in size between species, and in position and prominence within a species.

[12] ***Undulostrea***: the undulations of the shell margin are very different from the plications of other oysters.

[13] *Saccostrea*: hyote spines are present in juveniles only; chomata may be absent in some ecomorphs.

Table 3

Comparison of characters of the flesh and reproductive habits of genera and subgenera of living oysters.

Family	Subfamily	Tribe	Genus and subgenus	Mantle lobes thin[1]	Mantle lobes thick[1]	L promyal passage open[2]	R promyal passage wide[2]	R promyal passage narrow[2]	promyal passages closed[2]	Ht.-kid.-rec. complex gryphaeid[3]	Ht.-kid.-rec. complex ostreid[3]	Labial palp fusion long[4]	Labial palp fusion short[4]	No fusion of palp[4]	Anal appen. a bulbous collar[5]	Anal appen. a thin circular collar[5]	Anal appen. digitiform[5]	Anal appen. cardiform[5]	No anal appendage[5]	No accessory heart[6]	Accessory heart has tributaries[6]	Accessory heart lacks tributaries[6]	Broods larvae[7]
Gryphaeidae	Pycnodonteinae	**Hyotissini**	*Hyotissa*	X		X	X			X		X			X					X			?
			***Parahyotissa* s.s.**	X			X			X		X			X					X			?
			***P.* (*Pliohyotissa*)**	X			X			X		X			X					X			?
			***P.* (*Numismoida*)**	X			X			X		X			X					X			?
		Neopycnodontini	*Neopycnodonte*	X			X			X		X			X					X			?
Ostreidae	Lophinae	**Lophini**	*Lopha*	X					X		X	X					X				X		yes
			Alectryonella[8]	?	?				X		?	X					X				?		yes
			Dendostrea	X					X		X	X					X					X	yes
		Myrakeenini	***Myrakeena***		X				X		X		X					X				X	?
			Anomiostrea[9]																				
	Ostreinae	**Ostreini**	*Ostreola*		X				X		X		X				X					X	yes
			Ostrea s.s.		X				X		X		X					X			X		yes
			O. (*Eostrea*)		X				X		X		X					X			X		yes
			Nanostrea	X					X		X	X							?			X	?
			Planostrea	X					X		X		X			X						X	?
		Cryptostreini	***Cryptostrea***	X					X		X		X					X		?			yes
			Teskeyostrea	X					X		X		X						X	?			yes
			Booneostrea	X					X		X		X						X			X	yes
		Undulostreini	***Undulostrea***		X				X		X		X						X			X	?
		Pustulostreini	***Pustulostrea***		X				X		X	X						X				X	?
	Crassostreinae	**Striostreini**	*Saccostrea*		X			X			X		X						X			X	no
			Striostrea s.s.		X			X			X		X						X			X	?
			S. **(Parastriostrea)**		X			X			X		X						?			X	?
		Crassostreini	*Crassostrea*[10]		X			X			X			X					X			X	no

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[1] Mantle: thickness may be determined in part by age and nutritional state.

[2] Promyal passage: the left one is closed in all species but *Hyotissa hyotis*.

[3] Heart-kidney-rectum complex: in the gryphaeid condition the heart auricles are outpocketed, fused to the pericardium wall by their ventral surfaces, with very abundant brown granulocytes internally; the rectum distinctly penetrates the heart ventricle; the kidney is large, covering the dorsal curvature of the adductor muscle (which is circular in profile), with posterior caecum, and little outpocketing; renopores are at the dorsal ends of the anterior horns. In the ostreid condition, the auricles are not outpocketed, nor fused ventrally to the pericardium, and the amount of brown granulocytes is variable, but usually small; the rectum passes immediately behind the ventricle, the kidney is much reduced, with no large sac over the dorsal surface of the adductor muscle (which is reniform in profile), not posterior caecum, and the whole is much outpocketed as short, dendritic alveoli, with the renopores at the ventral ends of the anterior horns.

[4] Outer labial palp: the extent of fusion in the Ostreidae presents almost a continuous variable, but is here reduced to three alternatives.

[5] Anal appendage: this was difficult to determine in the limited amount of material available for some species (see text).

[6] Accessory heart: this was often difficult to determine precisely in the limited amount of preserved material available for some species.

[7] Reproductive habits: data are partly from the literature.

[8] Data on the flesh of *Alectryonella* are entirely from TORIGOE (1981).

[9] The flesh of *Anomiostrea* has not been available for study.

[10] *Crassostrea*: the labial palp is unfused, and there is no anal appendage in *C. virginica*, the genotype; but there is slight fusion of the palp, and a distinct circular flange on the anus in *C. gigas*.

St. Lawrence River estuary in eastern Canada (*O. rhizophorae* Guilding, 1827, is a junior synonym); in the eastern Pacific, *C. columbiensis* (Hanley, 1846) occurs from Ecuador northward to the Gulf of California (*O. corteziensis* Hertlein, 1951, is a junior synonym). *Crassostrea gigas* (Thunberg, 1793) occurs in the Indo-West Pacific from Pakistan to Japan and Korea, and in the Philippine Islands, Borneo, and Sumatra, but possibly not in the rest of Indonesia, or southward.

SUMMARY TABLES

Some of the more important characters which vary among Recent oysters are summarized in the preceding three comparative tables (pp. 153–155). The data refer to all known species of each genus and subgenus, not merely to the type species of the taxa cited, and they include variation found within the species. Therefore some characters which would seem to be mutually exclusive, as type of chomata in *Neopycnodonte, Alectryonella* and *Dendostrea,* and shape of the anal appendage and fusion of the labial palps in *Crassostrea,* appear in more than one column. For more precise information one must refer to the text.

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NOTE ADDED IN PROOF

While this paper was in press a paper was published with extensive descriptions, good photographs and many locality records of ***Parahyotissa*** (***Pliohyotissa***) *quercinus* (Sowerby, 1871), from the Gulf of California and southward to Manzanillo, Colima, Mexico: Gemmell, J., C. M. Hertz & B. W. Myers, 1985. A problem oyster in the Gulf of California ("*Ostrea*" *quercinus* Sowerby, 1871 rediscovered). Festivus (Publication of the San Diego, Calif., Shell Club) 17(5): 43–48.